

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

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Abstract

To investigate seasonal and annual interactions between management and grassland dynamics, a simple mechanistic model of the dynamics of production, structure and digestibility in permanent pastures was constructed. The model is designed to respond to various defoliation regimes, perform multiple-year simulations and produce simple outputs that are easy to use as inputs for a model of ruminant livestock production. Grassland communities are described using a set of average functional traits of their constituent grass groups. The sward is subdivided into four structural compartments: green leaves and sheath, dead leaves and sheath, green stems and flowers, and dead stems and flowers. Each compartment is characterized by its biomass, age and digestibility. Only above-ground growth is modelled, using a light-utilization efficiency approach modulated by a seasonal pattern of storage and mobilization of reserves. Ageing of plant parts is driven by cumulative thermal time from 1 January and by biomass flows. Age affects senescence, abscission and digestibility of green compartments and, therefore, the quality of green leaves and stems can increase or decrease over time in relation to net growth and defoliation dynamics. The functional traits having the greatest impact on model outputs are seasonal effects, period of reproductive growth and effects of temperature on photosynthetic efficiency.

The functional traits of the grass groups were parameterized for temperate pastures of the Auvergne region in France. The other model inputs are few: proportion of functional groups, basic weather data (incident photosynthetically active radiation, mean daily temperature, precipitation and potential evapotranspiration) and site characteristics (nitrogen nutri-

tion index, soil water-holding capacity). In the context of a whole-farm simulator, the model can be applied at a field scale.

Keywords: mechanistic dynamic model, permanent grassland, functional traits

Introduction

Understanding and predicting the dynamics of managed pastures at the field and farm scales could help define more sustainable management strategies for permanent pastures. Dynamic, mechanistic and deterministic models can greatly assist the investigation of this topic. According to Milne and Sibbald (1998), there is a need for models that (i) deal with permanent pastures with multiple objectives, (ii) predict daily biomass production, structure and quality in order to simulate selective defoliation and digestible energy as inputs for an animal production model, (iii) predict management-related changes in grassland dynamics over years and (iv) require few, easily collectable inputs.

Dynamic models of managed grasslands already exist. They usually predict daily growth as the product of potential growth and a number of functions of environmental factors (temperature, water and nutrient supply and season). In the earliest models, potential growth was determined empirically from the plant's genetic potential (Brown *et al.*, 1986) or from field measurements (Fick, 1980). More recent models (Moore *et al.*, 1997; Schapendonk *et al.*, 1998; Coléno and Duru, 1999; Herrmann and Schachtel, 2001; Bonesmo and Bélanger, 2002; McCall and Bishop-Hurley, 2003) have used a mechanistic approach, based on light-utilization efficiency, which enables a better understanding of seasonal dynamics of production. Several models predict the quality of the forage by estimating either the proportion of green and dead material (Fick, 1980; Brown *et al.*, 1986) or the digestibility of herbage, often in relation to the proportion of green leaves, stem and senescent material (Blackburn and Kothmann, 1989; Moore *et al.*, 1997; Bonesmo and

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Bélanger, 2002; Groot and Lantinga, 2004). The existing models are based on single species or growth forms, and the models that predict the behaviour of diverse pastures (Blackburn and Kothmann, 1989; Moore *et al.*, 1997) consider each species or growth form separately, which brings in a great complexity in inputs and outputs for highly diverse pastures.

The objective was to develop a model of permanent pasture, capable of simulating the effects of management (type and intensity) on biomass, structure and quality dynamics at the field scale. The model was designed for a whole-farm simulator, where it would be applied to each field. Therefore, the model had to be as simple as possible and had to produce outputs that could be used directly as inputs for an intake and production model of ruminant livestock. To keep the model simple, a functional approach instead of a species-based approach was chosen; it was assumed that the dynamics of permanent pastures could be explained by the average biological attributes (functional traits) of the plant community making up the grassland. This paper discusses the conceptual basis of the model and describes its equations and the parameterization procedure, with an analysis of model sensitivity to parameter values.

Conceptual basis of the model

The aim of the model was to predict the dynamics of permanent grasslands in an agricultural context. For this purpose, the model was based on the following five assumptions.

1. The functioning of a permanent pasture can be explained by the mean value of the biological attributes (functional traits) of its constituent grass groups. It was decided not to model each species separately because of the multitude of species and the limited knowledge available on interactions between species and on the functioning of secondary grasses and forbs other than legumes. The focus was on grasses because they constitute most of the standing biomass in permanent pastures in temperate areas (Louault *et al.*, 2005). Plants, and especially grasses, can be classified into functional groups according to their functional traits (Lavorel and Garnier, 1997). Recent studies have demonstrated that functional traits can not only be associated with production dynamics (Craine *et al.*, 2002) but also with environmental conditions (Diaz *et al.*, 1998) and specific responses to defoliation regimes (grazing: Bullock *et al.*, 2001; Diaz *et al.*, 2001; grazing and cutting: Louault *et al.*, 2005). Cruz *et al.* (2002) proposed a functional classification of grasses into four groups, based on vegetative and reproductive traits [mainly leaf dry-matter (DM) content], in a

similar way to Louault *et al.* (2005). Ansquer *et al.* (2004) used this functional classification to show that permanent pastures are made up of an association of functional groups and that the proportions of the functional groups in permanent pastures vary according to soil fertility and disturbance regime. In the model, a permanent pasture community is defined as an association, in constant proportions, of groups of species with similar functional traits (Lavorel and Garnier, 2002). As the aim was to develop a simple model, only one community per field is considered. The functional traits of the community were defined as the average of the functional attributes of the groups, defined by Cruz *et al.* (2002), weighted by the proportion of these groups in the community. By changing the proportions of the functional groups, a great variety of pasture communities can be simulated.

2. Sward heterogeneity can be described by the relative abundance of structural plant components, which is useful for explaining changes in sward quality and selective grazing. In the model, the sward is divided into four compartments representing the structural components of herbage (Carrère *et al.*, 2002): green leaves and sheath (green vegetative, GV), dead leaves and sheath (dead vegetative, DV), green stems and flowers (green reproductive, GR) and dead stems and flowers (dead reproductive, DR). Many authors (Terry and Tilley, 1964; Demarquilly and Chenost, 1969; Duru, 1997; Wilman and Rezvani Moghaddam, 1998) have shown that digestibility varies among plant parts, with leaves usually being more digestible than stems. Sward leafiness and stage of maturity, which can be determined by GV and GR content, respectively, have been extensively used as indicators of forage digestibility, nutritive value and voluntary intake (for reviews, see Fick *et al.*, 1994 and Demarquilly *et al.*, 1995). The differing digestibility of plant parts may explain why they are grazed selectively (Wallis de Vries and Daleboudt, 1994; Garcia *et al.*, 2003b).
3. In permanent pastures, growth, senescence and abscission can be described as continuous flows. Johnson and Parsons (1985) modelled sward dynamics using cohorts of leaves. At a sward scale, a cohort of leaves can be defined as a group of leaves that appear on the same day, and successively expand, mature and disappear together. As there is insufficient information to model each species separately in complex mixtures of grass and dicotyledonous species, it was decided to model continuous flows rather than cohort dynamics: the model calculates daily, at a field scale, the biomass flows in each structural compartment, given the environmental variables (Figure 1) and the average func-

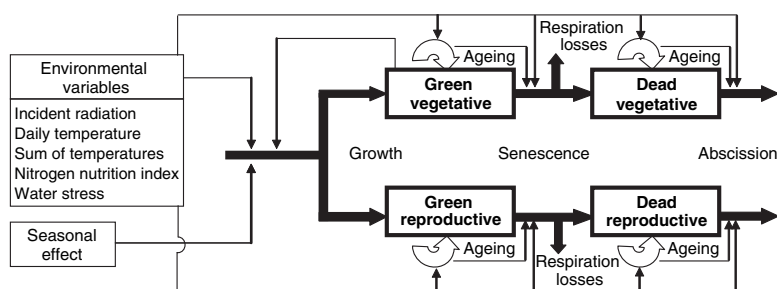


Figure 1 Flow diagram of the model: structural compartments of the sward are represented by boxes, biomass flows by thick arrows, and ageing functions by empty arrows. Thin arrows indicate direct and feedback effects of the various variables on the main flows.

tional traits of the community. Continuous flows have regularly been used to model grassland dynamics, for example, by Thornley and Johnson (1990).

4. In temperate regions, shoot growth is modulated by a seasonal pattern because of storage and mobilization of reserves in plant organs (for a review, see Volenec *et al.*, 1996). Growth is stimulated by mobilization of reserves and reduced by storage of reserves. Mobilization of reserves begins in early spring, peaks during vegetative growth and decreases during the reproductive period. In late summer and autumn, shoot growth is slowed down by storage of reserves and root growth (Bausenwein *et al.*, 2001). Protease activity in storage organs follows a similar pattern (Thornton and Bausenwein, 2000). This seasonal pattern was considered as a functional trait, because seasonal processes of storage and mobilization of reserves vary within grass groups; mobilization of reserves is higher for conservative grass species (e.g. *Dactylis glomerata*, *Agrostis capillaris* or *Festuca rubra*) and in low-fertility environments (Thornton *et al.*, 1993; 1994).
5. Quality of green compartments, senescence and abscission are affected by compartment ageing. During periods of rapid growth, such as in early spring, the sward is young because it is mainly composed of newly formed leaves, and the senescence rate is low. During the growing season, the lower the growth rate or the higher the biomass accumulation, the more the sward will age and the senescence rate will be higher. Duru and Ducrocq (2000) found that the senescence rate in swards of cocksfoot (*D. glomerata*) after cutting was initially very low and increased after 7–15 d of regrowth, with wide variation between seasons and years. It was hypothesized that a similar functioning for abscission in relation to age of dead tissues occurs. Demarquilly *et al.* (1995), like many other authors, measured a decrease in digestibility of green leaves and stems with ageing of the structural compartment. Fewer references exist on the digestibility of dead plant parts. Garcia *et al.* (2003a) found that it was fairly constant throughout the grazing season.

In the model, the digestibility of senescing compartments (DV and DR) is considered constant, while digestibility of green compartments (GV and GR) decreases with compartment age.

Model functions

Equations for compartment characteristics

Each compartment is described by its standing biomass (BM, kg DM ha⁻¹), age expressed in units of thermal time (AGE, degree-days, °C d) and organic matter digestibility (OMD).

Biomass of the green compartments is calculated daily as the difference between growth (GRO, kg DM ha⁻¹), distributed between GV and GR compartments with a reproductive function (REP), and senescence (SEN, kg DM ha⁻¹). Biomass of the dead compartments is calculated as the difference between senescence and abscission (ABS, kg DM ha⁻¹); σ_{GV} and σ_{GR} represent biomass losses through respiration during senescence (based on Ducrocq, 1996). The equations are

$$\frac{dBM_{GV}}{dt} = GRO_{GV} - SEN_{GV} \quad (1)$$

where

$$GRO_{GV} = GRO \times (1 - REP),$$

$$\frac{dBM_{GR}}{dt} = GRO_{GR} - SEN_{GR} \quad (2)$$

where

$$GRO_{GR} = GRO \times REP,$$

$$\frac{dBM_{DV}}{dt} = (1 - \sigma_{GV}) \times SEN_{GV} - ABS_{DV}, \quad (3)$$

and

$$\frac{dBM_{DR}}{dt} = (1 - \sigma_{GR}) \times SEN_{GR} - ABS_{DR}. \quad (4)$$

The mean age of the biomass in each compartment (AGE, °C d) is calculated daily as the weighted average of the age of the residual biomass and the age of the biomass entering the pool, which by definition is

considered to be zero. The age of the residual biomass is increased daily by the mean daily temperature ($T, ^\circ\text{C}$), if this temperature is positive. For each compartment, age can increase or decrease depending on the relative impacts of the inflow of new biomass and the ageing of old biomass. The equations are

$$\frac{d\text{AGE}_{\text{GV}}}{dt} = \frac{\text{BM}_{\text{GV}} - \text{SEN}_{\text{GV}}}{\text{BM}_{\text{GV}} - \text{SEN}_{\text{GV}} + \text{GRO}_{\text{GV}} \times (\text{AGE}_{\text{GV}} + T) - \text{AGE}_{\text{GV}}}, \quad (5)$$

$$\frac{d\text{AGE}_{\text{GR}}}{dt} = \frac{\text{BM}_{\text{GR}} - \text{SEN}_{\text{GR}}}{\text{BM}_{\text{GR}} - \text{SEN}_{\text{GR}} + \text{GRO}_{\text{GR}} \times (\text{AGE}_{\text{GR}} + T) - \text{AGE}_{\text{GR}}}, \quad (6)$$

$$\frac{d\text{AGE}_{\text{DV}}}{dt} = \frac{\text{BM}_{\text{DV}} - \text{ABS}_{\text{DV}}}{\text{BM}_{\text{DV}} - \text{ABS}_{\text{DV}} + (1 - \sigma_{\text{GV}}) \times \text{SEN}_{\text{GV}} \times (\text{AGE}_{\text{DV}} + T) - \text{AGE}_{\text{DV}}}, \quad (7)$$

and

$$\frac{d\text{AGE}_{\text{DR}}}{dt} = \frac{\text{BM}_{\text{DR}} - \text{ABS}_{\text{DR}}}{\text{BM}_{\text{DR}} - \text{ABS}_{\text{DR}} + (1 - \sigma_{\text{GR}}) \times \text{SEN}_{\text{GR}} \times (\text{AGE}_{\text{DR}} + T) - \text{AGE}_{\text{DR}}}. \quad (8)$$

The OMD of dead compartments (OMD_{DV} and OMD_{DR}) is constant, while the digestibility of green compartments decreases linearly with compartment age (AGE , $^\circ\text{C d}$). By definition, maximum digestibility (maxOMD) is the theoretical value at zero age and minimum digestibility (minOMD) is the theoretical value for maximum age, which are the leaf lifespan for GV (LLS , $^\circ\text{C d}$) and the duration of reproductive growth for GR (Duru, 1997). The duration of reproductive growth ($^\circ\text{C d}$) is the difference between the sum of temperatures at the end ($\text{ST}_2, ^\circ\text{C d}$) and at the beginning ($\text{ST}_1, ^\circ\text{C d}$) of the reproductive period. The equations are

$$\text{OMD}_{\text{GV}} = \text{maxOMD}_{\text{GV}} - \frac{\text{AGE}_{\text{GV}} \times (\text{maxOMD}_{\text{GV}} - \text{minOMD}_{\text{GV}})}{\text{LLS}} \quad (9)$$

and

$$\text{OMD}_{\text{GR}} = \text{maxOMD}_{\text{GR}} - \frac{\text{AGE}_{\text{GR}} \times (\text{maxOMD}_{\text{GR}} - \text{minOMD}_{\text{GR}})}{(\text{ST}_2 - \text{ST}_1)}. \quad (10)$$

Growth functions

Only the above-ground biomass is simulated. Total growth (GRO , kg DM ha^{-1}) is calculated daily as the product of the potential growth (PGRO , kg DM ha^{-1}) obtained in optimum conditions, a function represent-

ing growth limitation by environmental variables related to soil and climate characteristics (ENV), and a threshold function empirically accounting for the seasonal pattern of shoot growth because of reserve storage and mobilization (SEA). The equation is

$$\text{GRO} = \text{PGRO} \times \text{ENV} \times \text{SEA}. \quad (11)$$

Potential growth is calculated according to Schapendonk *et al.* (1998) as the product of incident photosynthetically active radiation (PAR_i , MJ m^{-2}), maximum radiation use efficiency (RUE_{max} , 3 g DM MJ^{-1} ; Schapendonk *et al.*, 1998) and a function of leaf area index (LAI) that accounts for the proportion of light intercepted by the sward. LAI is the product of specific leaf area (SLA , $\text{m}^2 \text{ g}^{-1}$), GV biomass (BM_{GV} , kg DM ha^{-1}) and percentage of laminae in GV ($\% \text{LAM}$). According to Schapendonk *et al.* (1998) and Bonesmo and Bélanger (2002), in the model the extinction coefficient is set at a constant value of 0.6 and potential growth (PGRO) is given by the equation

$$\text{PGRO} = \text{PAR}_i \times \text{RUE}_{\text{max}} \times [1 - \exp(-0.6 \times \text{LAI})] \times 10, \quad (12)$$

where

$$\text{LAI} = \text{SLA} \times \frac{\text{BM}_{\text{GV}}}{10} \times \% \text{LAM}.$$

Environmental limitation of growth (ENV) is the product of nutrition index (NI ; Bélanger *et al.*, 1992), which is a site-specific parameter, and three functions (Figure 2) accounting, respectively, for: (i) the decrease in RUE at light intensities higher than 5 MJ m^{-2} [$f(\text{PAR}_i)$, based on Schapendonk *et al.*, 1998]; (ii) photosynthesis activation when the 10-d moving average temperature ($T_{\text{m10}}, ^\circ\text{C}$) is above $T_0(^{\circ}\text{C})$ and photosynthesis stimulation by mean daily temperature ($T, ^\circ\text{C}$) [$f(T)$, following Schapendonk *et al.*, 1998] and (iii) growth limitation when water stress (W) increases [$f(W)$, following McCall and Bishop-Hurley, 2003]. The equation describing the environmental limitation of growth is

$$\text{ENV} = \text{NI} \times f(\text{PAR}_i) \times f(T) \times f(W). \quad (13)$$

Water stress (W) is given by the ratio of water reserves (WR , mm) to soil water-holding capacity (WHC , mm). The WR vary between zero and WHC ; precipitations (PP) fill the WHC , increasing WR , while actual evapotranspiration (AET , mm) empties it. It is considered that AET is equal to potential evapotranspiration (PET , mm) when the cover intercepts approximately 0.95 of the incident photosynthetically active radiation (PAR_i), that is when $\text{LAI} > 3$ (Johnson and Parsons, 1985), and that AET is proportional to LAI when the proportion of intercepted radiation is lower

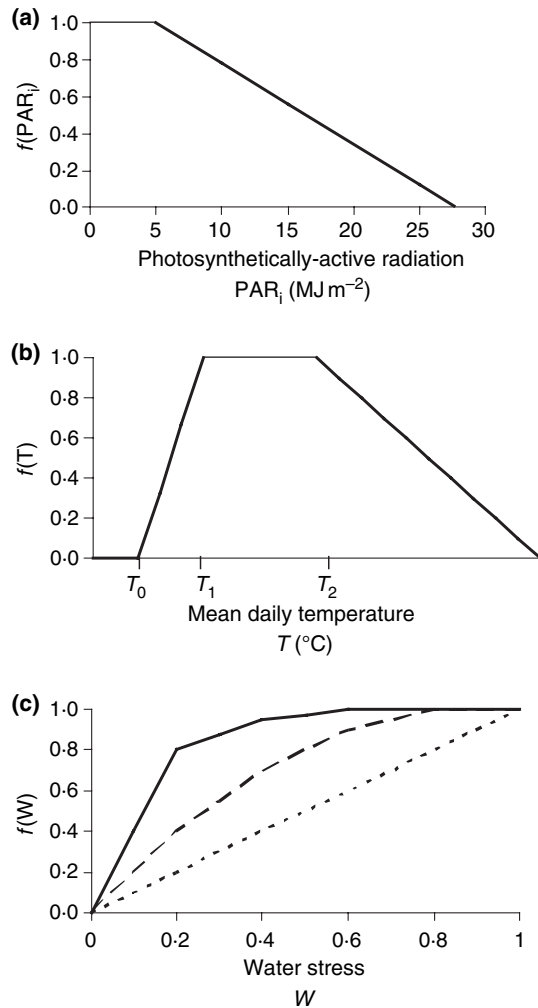


Figure 2 Threshold functions representing growth limitation exerted by three environmental variables: (a) $f(\text{PAR}_i)$ (Schapendonk *et al.*, 1998); (b) $f(T)$ (Schapendonk *et al.*, 1998); (c) $f(W)$ (McCall and Bishop-Hurley, 2003): solid line for $\text{PET} < 3.8$ mm, dashed line for $3.8 < \text{PET} < 6.5$ mm, and dotted line for $\text{PET} > 6.5$ mm. When functions reach 1.0, the corresponding environmental variable is not limiting for growth.

than 0.95 ($\text{LAI} < 3$). Water stress is described by the equation

$$W = \frac{\text{WR}}{\text{WHC}} \quad (14)$$

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

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

The seasonal effect (SEA; Figure 3) is an empirical function, drawn from information gathered from the literature (Thornton *et al.*, 1993; 1994; Volenec *et al.*, 1996; Thornton and Bausenwein, 2000; Bausenwein

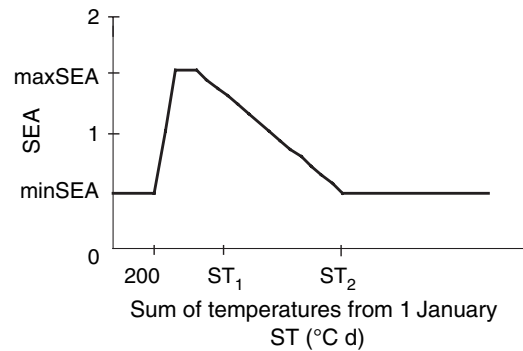


Figure 3 Seasonal effect (SEA) on growth, driven by the sum of temperatures from 1 January (ST). $\text{SEA} > 1$ indicates above-ground growth stimulation by mobilization of reserves; $\text{SEA} < 1$ indicates growth limitation by storage of reserves. SEA is equal to minSEA when $\text{ST} < 200$ °C d, then increases and reaches maxSEA when $(\text{ST}_1 - 200) < \text{ST} < (\text{ST}_1 - 100)$ ($\text{ST} = \text{ST}_1$ at the beginning of the reproductive period). During summer, SEA decreases, returning to minSEA at ST_2 ($\text{ST} = \text{ST}_2$ at the end of the reproductive period). minSEA and maxSEA are functional traits, arranged symmetrically around 1: $(\text{minSEA} + \text{maxSEA})/2 = 1$.

et al., 2001), because there are few data available on the dynamics of storage and mobilization of reserves for the many species that constitute permanent grasslands. In the model, SEA is low during autumn and winter. It increases from the onset of growth, i.e. when the cumulated thermal time from 1 January (ST, °C d) is above 200 °C d and reaches a peak (maxSEA) when $\text{ST}_1 - 200 < \text{ST} < \text{ST}_1 - 100$, before the period of reproductive growth. During summer, it decreases linearly with thermal time, returning to its minimum value (minSEA) at the end of the reproductive period, when $\text{ST} = \text{ST}_2$.

Reproductive growth is determined by the REP function and driven by ST; it begins at ST_1 (°C d) and ends at ST_2 (°C d). Before and after the period of reproductive growth, REP is set to zero. During the period of reproductive growth, REP is a function of the NI, as it has been shown that the proportion of stem in the herbage depends on the level of nitrogen nutrition (Duru *et al.*, 2000). The minimum NI has been set to 0.35 (Bélanger *et al.*, 1994) and the associated minimum GR growth rate to 0.25 (Balent *et al.*, 1997). A boolean function (CUT) stops reproductive growth ($\text{CUT} = 0$) if defoliation occurs when $\text{ST}_1 < \text{ST} < \text{ST}_2$. The REP function is

$$\text{REP} = \left[0.25 + \frac{(1 - 0.25) \times (\text{NI} - 0.35)}{1 - 0.35} \right] \times \text{CUT}. \quad (15)$$

As second-cycle reproductive growth is a limited phenomenon in permanent pastures in temperate regions, it is not included in the model for simplicity.

Senescence and abscission functions

Senescence (SEN, kg DM ha⁻¹) is proportional to green biomass, mean daily temperature (T , °C) and basic senescence rates (K , based on Ducrocq, 1996). When T exceeds the minimum temperature for growth (T_0 , °C), senescence is proportional to T and stimulated by pool-ageing through the functions described in Figure 4. For temperatures between zero and T_0 , no senescence occurs. When temperature drops below zero, senescence is driven by freezing effects and is proportional to $|T|$. The senescence equations are

$$\text{SEN}_{\text{GV}} = K_{\text{GV}} \times \text{BM}_{\text{GV}} \times T \times f(\text{AGE}_{\text{GV}}) \text{ if } T > T_0, \\ \text{and similarly for compartment GR} \quad (16)$$

and

$$\text{SEN}_{\text{GV}} = K_{\text{GV}} \times \text{BM}_{\text{GV}} \times |T| \text{ if } T < 0, \\ \text{and similarly for compartment GR.} \quad (17)$$

Abscission of dead tissues (ABS) is proportional to senescing biomass, mean daily temperature (T , °C) and basic rates of abscission (K), based on Ducrocq, 1996). Abscission only occurs when T is above zero and is

stimulated by pool-ageing through the functions described in Figure 4:

$$\text{ABS}_{\text{DV}} = \text{KL}_{\text{DV}} \times \text{BM}_{\text{DV}} \times T \times f(\text{AGE}_{\text{DV}}) \text{ and,} \\ \text{similarly, for compartment DR.} \quad (18)$$

Harvested biomass

The model simulates standing biomass (BM, kg DM ha⁻¹). To predict harvested biomass (hBM), the pasture is considered to be cut 0.05 m above ground level. The residual biomass after cutting (resBM, kg DM ha⁻¹) in each structural compartment (Eq. 19) is calculated using herbage bulk densities (BD, g DM m⁻³), then the biomass harvested in each structural compartment is calculated as the difference between standing and residual biomass:

$$\text{resBM}_{\text{GV}} = 0.05 \times 10 \times \text{BD}_{\text{GV}} \text{ and, similarly,} \\ \text{for compartments GR, DV and DR.} \quad (19)$$

Finally the total harvested biomass (hBM) is calculated as the sum of the biomass harvested in each compartment, and the digestibility of harvested forage as the weighted average of the digestibility of the structural compartments. For greater realism, it is assumed that during harvest, 0.10 of the harvestable biomass in each structural compartment is lost.

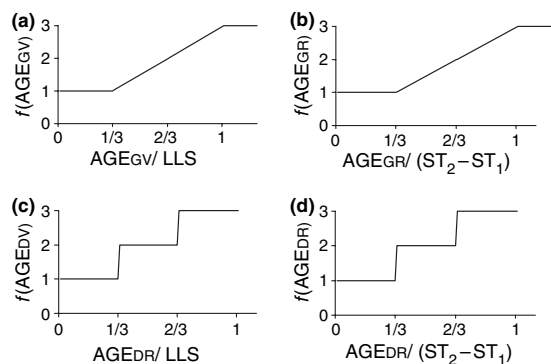


Figure 4 Effect of compartment age (AGE, °C d) on senescence functions (a and b) and abscission functions (c and d). AGE effect is assumed to be linear for senescence but non-linear for abscission, as leaves yellow and die progressively, but fall at once. Senescence of the green vegetative (GV) and green 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.

Model parameterization and sensitivity analysis

Model parameters associated with functional traits

In the model, a site is described by its NI, WHC and community, which is defined by the relative abundance of the four functional groups described in Table 1. Model functions are based on NI, WHC and twenty-two parameters associated with functional traits of the community and calculated as the weighted average of the parameter values of the four functional groups. Eleven parameters are related to growth functions: rates of biomass loss with respiration (σ_{GV} and σ_{GR}), SLA (m² g⁻¹), percentage of laminae in GV (%LAM), threshold temperatures for growth (T_0 , T_1 , T_2 , °C), sum of temperatures profiling the period of reproductive growth (ST_1 and ST_2 , °C d) and maximum and minimum seasonal effect on growth (maxSEA and minSEA). Five parameters deal with senescence, abscission and ageing: basic senescence (K_{GV} and K_{GR}) and abscission (KL_{DV} and KL_{DR}) rates and leaf lifespan (LLS, °C d). Six parameters indicate the digestibility of dead compartments (OMD_{DV} and OMD_{DR} , g g⁻¹) and green compartments

Table 1 Functional groups for grass species in the classification of Cruz *et al.* (2002).

	Rich/fertile sites	Poor/infertile sites
Frequent defoliation	Group A: high specific leaf area and high digestibility, short leaf lifespan, early reproductive growth	Group C: low specific leaf area and medium digestibility, long leaf lifespan, medium-to-late reproductive growth
Infrequent or lenient defoliation	Group B: medium specific leaf area and high digestibility, long leaf lifespan, medium-to-late reproductive growth	Group D: low specific leaf area and low digestibility, very long leaf lifespan, very late reproductive growth

(maxOMD_{GV}, minOMD_{GV}, maxOMD_{GR} and minOMD_{GR}, g g⁻¹). Bulk densities of the structural compartments (BD_{GV}, BD_{GR}, BD_{DV} and BD_{DR}) determine the vertical distribution of biomass.

The functional groups: a framework for model parameterization

According to Cruz *et al.* (2002), temperate grasses can be classified into four groups on the basis of their functional traits (Table 1):

1. Group A comprises species found in fertile sites, adapted to frequent defoliation (e.g. *Lolium perenne*). Characteristic traits include high SLA and high digestibility, short leaf lifespan and early reproductive growth and flowering.
2. Group B comprises species found in medium-to-fertile sites, with infrequent defoliation (e.g. *D.*

glomerata). Characteristic traits include a medium SLA and high digestibility, and long leaf lifespan.

3. Group C comprises species found in medium-to-poor sites, resistant to defoliation (e.g. *A. capillaris* and *F. rubra*). Characteristic traits include low SLA and medium digestibility, long leaf lifespan and late reproductive period and flowering.
4. Group D comprises species found in poor sites with infrequent defoliation (e.g. *F. ovina* and *Nardus stricta*). Characteristic traits include low SLA and low digestibility, very long leaf lifespan and late reproductive period and flowering.

Parameterization of the four functional groups

The parameterization of groups A–D is given in Tables 2 and 3. Some functional traits (SLA, %LAM, ST₁, ST₂, LLS) were directly measured by Cruz *et al.* (2002),

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.

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.

Ansquer *et al.* (2004) and Louault *et al.* (2005). For the other traits, values were selected from the literature, preferably from measurements carried out in the Auvergne region of France. When regional data were not available, the values of the traits were set constant whatever the functional group (Table 3). The bulk densities of the structural compartments were parameterized using measurements on various grassland communities, differing in their dominant functional group and management regime. For functional groups A and B, rich well-managed pastures were used. These pastures contain a high proportion of green herbage and, therefore, the bulk density is higher for green than for dead compartments. The opposite situation is found in less productive and less well-managed pastures, which were used to set bulk densities for groups C and D.

Model sensitivity to functional traits

Sensitivity analysis was performed on a grassland community composed of 0.20 of group A, 0.30 group B and 0.50 group C, with NI set at 0.75 and WHC at 60 mm. The values of each functional trait were successively altered by $\pm 10\%$ and model response to these changes was measured under a simple management regime consisting of three cuts (cut 1 on 30 June, cut 2 on 25 August and cut 3 on 30 October). The model was run for eight years (1993–2000) using weather data recorded at an INRA Research Station in Auvergne,

France (Marcenat, altitude 1100 m asl). The average sensitivity was considered over years at each cutting date. With the standard values of the functional traits, the model predicted harvested biomass of 3.80, 1.83 and 0.74 t DM ha⁻¹, values of forage OMD of 0.74, 0.68 and 0.78, and a green herbage content of 0.50 GV + 0.34 GR, 0.69 GV and 0.95 GV for the first, second and third cuts respectively. The remaining dead herbage was essentially composed of DV.

Model sensitivity was assessed with normalized sensitivity coefficients (NSC), defined as the ratio between the rate of variation of the output variable and the rate of variation of the parameter. As NSC for positive and negative alterations were similar, a single sensitivity indicator is given for each functional trait in Table 4. As results for the third cut were similar to those of the second cut, they are not shown.

The functional traits having the greatest impact on model outputs were the seasonal effect, period of reproductive growth and the temperature effect on photosynthetic efficiency. Harvested biomass was most sensitive to the seasonal effect (maxSEA and minSEA) and to the minimum temperature for optimum growth (T_1); it was also sensitive to leaf area (SLA) and percentage of laminae in compartment GV (%LAM). OMD was mainly sensitive to maximum and minimum digestibility (max- OMD_{GV} , min OMD_{GV}) in compartment GV. Structural composition of the herbage was sensitive at the first cut to the sum of temperatures from the beginning of the reproductive period (ST_1), the minimum temperature for optimal growth (T_1) and leaf traits (SLA, %LAM); and at the second cut to the sum of temperatures to the end of the reproductive period (ST_2) in relation to the seasonal effect. In the range of conditions tested, model outputs showed almost no sensitivity to functional traits related to the reproductive compartments.

Discussion

The model predicts production, structure and quality dynamics for managed permanent pastures, using a simple mechanistic approach based on the average functional traits of the grassland community. The biomass is subdivided into four compartments, representative of the structural components of herbage (Carrère *et al.*, 2002). Each compartment is described according to its biomass, age and digestibility. Above-ground growth is assumed to be affected by a seasonal pattern because of the dynamics of storage and mobilization of reserves. The quality of the green compartments, senescence and abscission are assumed to depend on the ageing of a compartment. This section is aimed at discussing the modelling choices, and especially the functional, structural and mechanistic approaches used.

Table 4 Model sensitivity to functional traits: average results for eight simulated weather years for harvested biomass (hBM), organic matter digestibility (OMD) and proportion of compartments green vegetative (GV) and green reproductive (GR) (for cuts 1 and 2) under a simple management consisting of three cuts (results of cut 3 not shown).

Functional trait	Values used for grassland community	Sensitivity: cut 1				Sensitivity: cut 2		
		hBM	OMD	Proportion of GV	Proportion of GR	hBM	OMD	Proportion of GV
σ_{GV}^*	0.4	–	n.s.	+	+	–	+	+
σ_{GR}	0.2	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
SLA	0.0256 m ² g ^{–1} DM	++	n.s.	n.s.	--	+	n.s.	–
%LAM	0.68	++	n.s.	n.s.	--	+	n.s.	–
T_0	4°C	--	n.s.	n.s.	+	n.s.	n.s.	n.s.
T_1	10°C	---	+	n.s.	++	–	n.s.	n.s.
T_2	20°C	n.s.	n.s.	n.s.	n.s.	+	n.s.	n.s.
ST ₁	775°C d	n.s.	n.s.	+++	---	n.s.	n.s.	–
ST ₂	1450°C d	+	n.s.	n.s.	+	+	–	--
MaxSEA	1.33	+++	n.s.	n.s.	–	+	n.s.	–
MinSEA	0.67	+	n.s.	n.s.	–	+++	n.s.	–
K_{GV}	0.002°C ^{–1}	--	n.s.	--	+	–	n.s.	–
K_{GR}	0.001°C ^{–1}	n.s.	n.s.	n.s.	–	n.s.	n.s.	n.s.
Kl_{DV}	0.001°C ^{–1}	–	n.s.	+	+	–	+	+
Kl_{DR}	0.0005°C ^{–1}	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
LLS	790°C d	+	n.s.	+	–	+	+	+
OMD _{DV}	0.45	0	n.s.	0	0	0	+	0
OMD _{DR}	0.40	0	n.s.	0	0	0	n.s.	0
MaxOMD _{GV}	0.88	0	+	0	0	0	++	0
MinOMD _{GV}	0.66	0	+	0	0	0	+	0
MaxOMD _{GR}	0.88	0	+	0	0	0	n.s.	0
MinOMD _{GR}	0.49	0	n.s.	0	0	0	n.s.	0
BD _{GV}	1025 g DM m ^{–3}	n.s.	n.s.	–	n.s.	n.s.	–	–
BD _{GR}	1150 g DM m ^{–3}	n.s.	n.s.	n.s.		n.s.	n.s.	n.s.
BD _{DV}	250 g DM m ^{–3}	–	n.s.	+	+	–	n.s.	+
BD _{DR}	225 g DM m ^{–3}	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

σ_{GV} and σ_{GR} , rates of biomass loss with respiration; SLA, specific leaf area; %LAM, percentage of laminae; T_0 , T_1 , T_2 , threshold temperatures for growth; ST₁ and ST₂, initial and end reproductive growth temperatures, respectively; maxSEA and minSEA, maximum and minimal seasonal effects, respectively; 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; LLS, leaf lifespan; OMD, organic matter digestibility; BD, bulk densities.

Positive or negative signs indicate the level of correlation between input parameter and output variable; '+++’ and ‘---’ indicate NSC > 1 and NSC < –1, respectively; ‘++’ and ‘--’ indicate 0.5 < NSC < 1 and –1 < NSC < –0.5, respectively; ‘+’ and ‘–’ indicate 0.1 < NSC < 0.5 and –0.5 < NSC < –0.1, respectively; n.s. indicates –0.1 < NSC < 0.1; and indicate NSC = 0, due to the structure of the model.

Can permanent grassland be reduced to a set of average functional traits?

Functional traits have already been used for modelling grass growth. For example, LAI has been used when an approach using light-utilization efficiency has been chosen (Moore *et al.*, 1997; Schapendonk *et al.*, 1998; Coléno and Duru, 1999; Herrmann and Schachtel, 2001; Bonesmo and Bélanger, 2002). Representing complex grassland communities with average traits is

consistent with previous models. Moore *et al.* (1997) used similar functions to predict growth, senescence and abscission dynamics for annual and perennial grasses and forbs, and Blackburn and Kothmann (1989) were able to simulate grass and forb dynamics from equations established for grasses by adjusting growth, senescence and abscission rates, and biomass losses via respiration.

The functional approach used reduces model inputs to a minimum (NI, WHC, proportion of functional

groups and sward state at the beginning of the simulation). The main drawback of this approach is the difficulty in parameterization of certain functional traits. Traits to which the model is not sensitive can be set as constants without altering the accuracy of model, but traits to which the model is very sensitive should ideally be carefully estimated. The model is particularly sensitive to the seasonal effect, which is difficult to estimate, because the function of seasonal growth is empirical and remains poorly documented in the literature. The low sensitivity to traits related to reproductive growth is probably due to the range of conditions where the model was tested: in more extensive situations, with late or low herbage utilization (e.g. late first cut), the results would have been different.

The model has been parameterized for temperate pastures of the Auvergne region in France. To apply the model to other grasslands, the parameterization of the four functional groups from Cruz *et al.* (2002) should be adjusted to habitat and management conditions, because of species plasticity (Garnier *et al.*, 2001; Al Haj Khaled *et al.*, 2005). However, while the exact values of the parameters may vary between sites, species ranking remains unchanged (Lavorel and Garnier, 2002; Al Haj Khaled *et al.*, 2005). Clearly, the model was not designed for tropical grasslands or grasslands containing a high proportion of forbs or shrubs. In most well-exploited grasslands of the Auvergne region in France, forbs and legumes constitute less than 0.20 of the standing biomass.

Value of a simple, predominantly mechanistic, approach

Considering that the model was built for a whole-farm simulator, it develops a simple mechanistic approach to grassland dynamics, based on (i) the functional description of grassland, (ii) the subdivision of the sward into four interacting structural compartments, (iii) the light-utilization efficiency approach to growth and (iv) the temperature- and age-driven senescence and abscission functions. The morphological and physiological approaches to growth and quality dynamics are kept extremely simple in the model; more complex models describing nutrient flows and morphological stages of the grass tillers have been developed, e.g. by Thornley and Johnson (1990) and Groot and Lantinga (2004).

Without the empirical function representing the seasonal effect on growth, the model would not reproduce the peak of growth in spring and the low autumn growth observed in the grasslands of Auvergne, France. McCall and Bishop-Hurley (2003) and Dolling *et al.* (2005) also used an empirical function of time of year to influence shoot growth dynamics for

grasses and lucerne respectively. Using an empirical function could alter model predictions of year-to-year variability for contrasted weather scenarios or extreme management regimes. Actually, growth stimulation by mobilization of reserves in a given year depends on the amount of energy stored the year before, which is a function of photosynthetic activity, and thus of weather and management conditions (Volenec *et al.*, 1996). In the model of Herrmann and Schachtel (2001), based on a sink/source approach, growth can be stimulated by mobilization of reserves from previously stored matter.

Sward structural composition: a tool for predicting changes in digestibility of herbage and for interacting with a model of selective grazing

Dividing the sward into structural compartments is a simple tool for explaining changes in the digestibility of herbage over time. Relating digestibility of herbage to age makes it possible for the digestibility of a given compartment to increase or decrease over time depending on net growth and defoliation dynamics. Such a description of the sward also enables direct interactions with a model of selective defoliation, because grazers' preferences can be related to the abundance and quality of plant structural components (Baumont *et al.*, 2005). Similar approaches have been used in previous models, mainly with the objective of evaluating herbage quality and modelling diet selection. Blackburn and Kothmann (1989) divided the sward into green, old and dead vegetative matter, and reproductive matter. Herrmann and Schachtel (2001) considered separately leaf, stem, ear and dead material. Bonesmo and Bélanger (2002) modelled green leaves, dead leaves and stem, and McCall and Bishop-Hurley (2003) differentiated green and dead biomass.

To keep the model simple, sward heterogeneity was represented only by the relative abundance of structural components, without spatial arrangement. Hence, the predictions of the model could be less accurate in situations where the spatial arrangement of the sward plays an important role in vegetation dynamics, e.g. in extensively grazed pastures (Baumont *et al.*, 2005).

Conclusion

The originality of the model described here lies in the combination of two simple approaches to grasslands: functional – based on the average functional traits of the grassland community – and structural – based on the distinction between vegetative and reproductive, i.e. green and dead matter. The model should enable the simulation of the dynamics of biomass, structure and digestibility of herbage at the field and farm scales

for a wide range of grassland communities and management regimes. Once functional group parameters are calibrated, there are few other model inputs: proportion of functional groups, basic weather data (incident photosynthetically active radiation, mean daily temperature, precipitation, potential evapotranspiration) and site characteristics (nitrogen nutrition index, soil water-holding capacity). Model outputs are simple (biomass and digestibility of the four structural compartments) and can be readily used as inputs for an intake and production model for ruminant livestock. The model's behaviour and its ability to reproduce the dynamics of permanent pastures under various cutting regimes and to perform multiple-year simulations are discussed in a companion article (Jouven *et al.*, 2006).

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