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MODELING GROWTH OF STAR GRASS (*Cynodon plectostachyus*) IN THE SUBTROPICAL REGIONS OF CENTRAL MEXICO

[SIMULANDO EL CRECIMIENTO DEL PASTO ESTRELLA (*Cynodon plectostachyus*) EN LAS REGIONES DE CLIMA SUBTROPICAL DEL CENTRO DE MEXICO]

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SUMMARY

The present work describes a mathematical model that simulates growth and biomass production of Star grass in the lowland subtropical areas of Central Mexico. The Star grass model simulates growth of the different plant structures such as the root, stem and shoots, and it has five submodels: growth, photosynthesis, mineral intake, ontogenic and disturbances submodels. The growth submodel simulates nutrient partition and growth of root, stem and leaves. The photosynthesis submodel simulates the transformation of solar energy and carbon into biomass, and it is determined by irradiation, ambient temperature and the leaf area index. The mineral uptake submodel represents the interphase between the soil and the plant, and it simulates a plant's uptake of nitrogen and phosphorous as well as the different factors that determined their availability, such as soil water content and the mineralization rate. The ontogenic submodel emulates the vegetative phase and the senescence of the plant. The disturbances submodel simulates the effect of factors such as harvest, fire and grazing on the above-ground part of the plant. The original model was developed for C3 plants so it was necessary to modify its parameters for simulating a C4 plant like Star grass. The parameters of soil, drought tolerance, nitrogen content (in the degradable fraction of the plant) and temperatures for maximum and minimum plant growth were modified. The phenological phase of the plant was modified and the reproductive routine was eliminated since Star grass is propagated by stolons and generally remains in the vegetative stage. The re-growth of new shoots begins when soil temperature is above 11^{o} C and soil water content above 0.5. Minimum data set for model development was collected from a sward planted with Star grass and located in the Tejupilco municipality (18º 45´ 30" North and 99º 59´ 07" West) México, and data from literature was also used. Daily climate data was obtained from the local meteorological station. Model predictions were validated with data sets collected from two more swards located in the same region. Results indicated that the model's predicted dry matter yield during the entire production cycle was very close to observed data (R^2=0.92, P<0.05), and also that precision was high because observed and predicted regression lines were almost overlapping. Model predictions for the other two paddocks were also very close to observed values (R^2=0.88 and R^2=0.96, P<0.05). It was concluded that the Star grass model was successful in predicting dry matter yield for a Star grass paddock located in the lowland areas of central Mexico.

Key words: Star grass; mathematical model; Mexico.

RESUMEN

El presente trabajo describe el desarrollo matemático de un modelo que simula el crecimiento y producción del Pasto Estrella bajo pastoreo continuo en las regiones subtropicales del centro de México. El modelo de pasto estrella simula el crecimiento de las diferentes estructuras de la planta tales como la raíz, el tallo, y los rebrotes y se compone de 5 submodelos: crecimiento, fotosíntesis, absorción de minerales, fenología y un submodelo que simula las perturbaciones que sufre la planta. El submodelo de crecimiento simula la partición de nutrientes y crecimiento de la raíz, tallo y hojas. El submodelo fotosíntesis simula la transformación de la energía solar y carbón en biomaas, lo cual está determinado por la irradiación, la temperatura ambiental y el índice de área foliar. El submodelo de absorción de los minerales representa la interfase entre el suelo y la planta y simula la absorción de nitrógeno y fósforo así como los diferentes factores que determina su disponibilidad, tales como el contenido de agua en el suelo, y la tasa de mineralización. El submodelo fenológico simula la fase vegetativa y la senescencia de la planta. El submodelo de perturbaciones el efecto de factores tales como la cosecha, el fuego y el pastoreo sobre la parte aérea de la planta. El modelo original fue desarrollado para plantas del tipo C3 así que fue necesario modificar sus parámetros para simular planta tipo C4 como el pasto estrella. Los parámetros del suelo, tolerancia a la sequía, contenido de nitrógeno (en la parte degradable de la planta) y las temperaturas para el crecimiento mínimo y máximo de la planta fueron modificados. Las etapas fenológicas de la planta fueron modificadas y la rutina reproductiva fue eliminada dado que el pasto estrella es propagado vía estolones y generalmente permanece en estado vegetativo. El retoño de las hojas nuevas inicia cuando la temperatura del suelo está por arriba de los 11 oC y el contenido de agua en el suelo está por arriba de 0.5. Los juegos mínimos de datos para el desarrollo del modelo fue colectado de una pradera sembrada con pasto estrella ubicada en el municipio de Tejupilco (18º 45´ 30” norte y 99º 59´ 07” oeste) México, también se emplearon datos de tomados de la literatura especializada. Datos sobre el clima fueron obtenidos de una estación meteorológica local. Las predicciones del modelo fueron validados con juegos de datos recolectados en dos praderas localizadas en la misma región de estudio. Los resultados indican que las predicciones del modelo para producción de materia seca durante el ciclo de producción del pasto estrella fueron muy cercanas a los datos observados (T2=0.92, P<0.05), también la precisión de modelo es adecuada. Las predicciones del modelo para las otras dos praderas fueron también muy cercanas a los valores observados en campo (R2=0.88 and R2=0.96, P<0.05). Se concluyó que el modelo de pasto estrella fue exitoso en predecir la producción de materia seca para una pradera de pasto estrella ubicada en las regiones subtropicales del centro de México.

Palabras clave: Pasto estrella; modelo matemático; México.

INTRODUCTION

Star grass (SG) (*Cynodon plectostachyus*) is the most widespread grass in the tropical climate regions of Mexico and Latin America (Caro-Costas *et al*. 1976, Gredpac 1990, Manson and Burton 1982, Ortega and Gonzalez 1990). Agronomic characteristics of SG allow it to adapt to different soil types, to resist grazing, to grow rapidly and to response adequately to fertilization. It competes well with other grasses and weeds due to its aggressive growth and rapid propagation (Clayton and Harlan 1970, Pozo *et al*., 2000; Porto *et al*., 2009).

In the Northern hemisphere the largest volume of dry matter production of SG is observed during the rainy season (June to October), production declines during the dry season (February to May) and the lowest yield occurs during the winter (November to March), as SG growth is sensitive to low temperatures and a short photoperiod (Ludlow 1985).

Nutritional characteristics of SG vary significantly throughout the year because they are determined by climate conditions and plant maturity. López *et al*. (2010) investigated the nutritional characteristics of the SG grown in the tropical region of central Mexico. These authors observed that crude protein (CP) content and dry matter digestibility of SG passed from 15% and 65% in June to 4% and 50% in February, respectively. These variations in the nutritional characteristics of SG point to the need for adequate management practices with both the grass and the cattle that graze it. *In vivo* evaluation of alternative management practices requires substantial amount of resources including several paddocks cultivated with SG and a large number of animals (e.g. cows) to evaluate their productive response to different stocking rates and feeding strategies based on this grass. Even if these resources were available, several years of work are needed to arrive at conclusive results.

Modeling SG growth and production offers the possibility to evaluate alternative production strategies under different climate and management scenarios. Different grass models have been developed, for example, Johnson and Thornley (1985) developed a model for a temperate climate grass like the ryegrass, Herrero *et al*. (2000) developed a model for Kikuyu grass (*Pennisetum clandestinum*), a sub-tropical grass, Silveira (1999) developed a multi-grass species model for temperate climates. However, there are no models published in the literature for SG, even though it is one of the most widespread grasses in the world’s tropical regions.

Therefore, the objective of the present work was to develop a mathematical model that simulates growth of a vegetative sward of Star grass.

MATERIALS AND METHODS

Model description

The SG model was derived from the ryegrass model developed by Silveira (1999). Silveira's model is based on the model developed by Johnson and Thornley (1983, 1984, 1985, 1987) that simulates Ryegrass growth in temperate climates (Thornley and Verberne 1989, Moore *et al*. 1997). The model was built in Model Maker software (Zethon Tech, Nottingham, 1994, UK) and it simulates growth, nutrient partitioning, plants' respiration flow between categories, mineral absorption, senescence, grazing and management practices such as the use of fire to eliminate dead standing material. The SG model is subdivided into five submodels: grass, soil, animals and climate. This paper describes the structure and functioning of the grass submodel, and its general structure is outlined in Figure 1.

The grass submodel is divided into roots (**R**), and stems + shoots (**Sh),** all in four age categories (Figure1). The main changes introduced to the Johnson and Thornley (1984) model in order to make it simulate SG are:

1. The original parameters used to simulate C3 plants were changed in the SG model in order to simulate a C4 plant. The parameters changed are: drought tolerance coefficient, fractional nitrogen content in degradable structure, maximum and minimum temperature for positive plant activity, minimum N soil content without affecting mobility, optimum temperature for positive plant activity and maximum growth rate.

2. For modeling purposes it was assumed that SG plants remain permanently in a vegetative stage because their propagation is by stolons and not by seeds (Mislevy *et al*. 1989; Mislevy and Brown 1991). Thus, to simulate the vegetative growth of SG the subroutine used in the Johnson and Thornley (1985) and Thornley and Verbena (1989) models for vegetative growth was used in the present SG model.

3. The lineal effect of temperature on plant growth described by Johnson and Thornley (1984) and used in the Johnson and Thornley (1985) model was replaced by a bell function as described by Hanson *et al.* (1988). This bell function is more adequate for simulating C4 plants because, as mentioned by Hanson et al. (1988), the lineal function is more appropriate for plants growing in temperate climates and the SG is a tropical plant.

4. A new subroutine was introduced to calculate the Angot value, which is used in the SG model to calculate extraterrestrial solar radiation and plant photosynthesis.

5. A subroutine that simulates absorption and utilization of phosphorous by the plant was introduced.

6. A subroutine that simulates the intake by animals of the different fractions of plants (e.g. leaves and stems of different compartments) was introduced.

Model Structure

Symbols and definitions of variables and parameters used in the model are given in the Appendix. The model assumes that above-ground dry matter weight occupies the eight compartments described by Johnson and Thornley (1983): growing sheath-stem, growing leaves, first fully expanded sheath-stem, first fully expanded leaves, second fully expanded sheath-stem, second fully expanded leaves, senescing sheath-stem, and senescing leaves, plus a new compartment added by Silveira (1999) that describes standing dead material (Figure 1). Every live leaf compartment has one corresponding leaf area index compartment. Each nutrient simulated in the model has a soluble pool, C from photosynthesis, and N and P from soil uptake flow into the model through respective soluble compartments. Roots are considered in the same way as the above-ground material representing the transition from growing to dead roots, as in Thornley and Verberne (1989). However, roots were split into two types, structural and active roots (Figure 1), as in Silveira (1999).

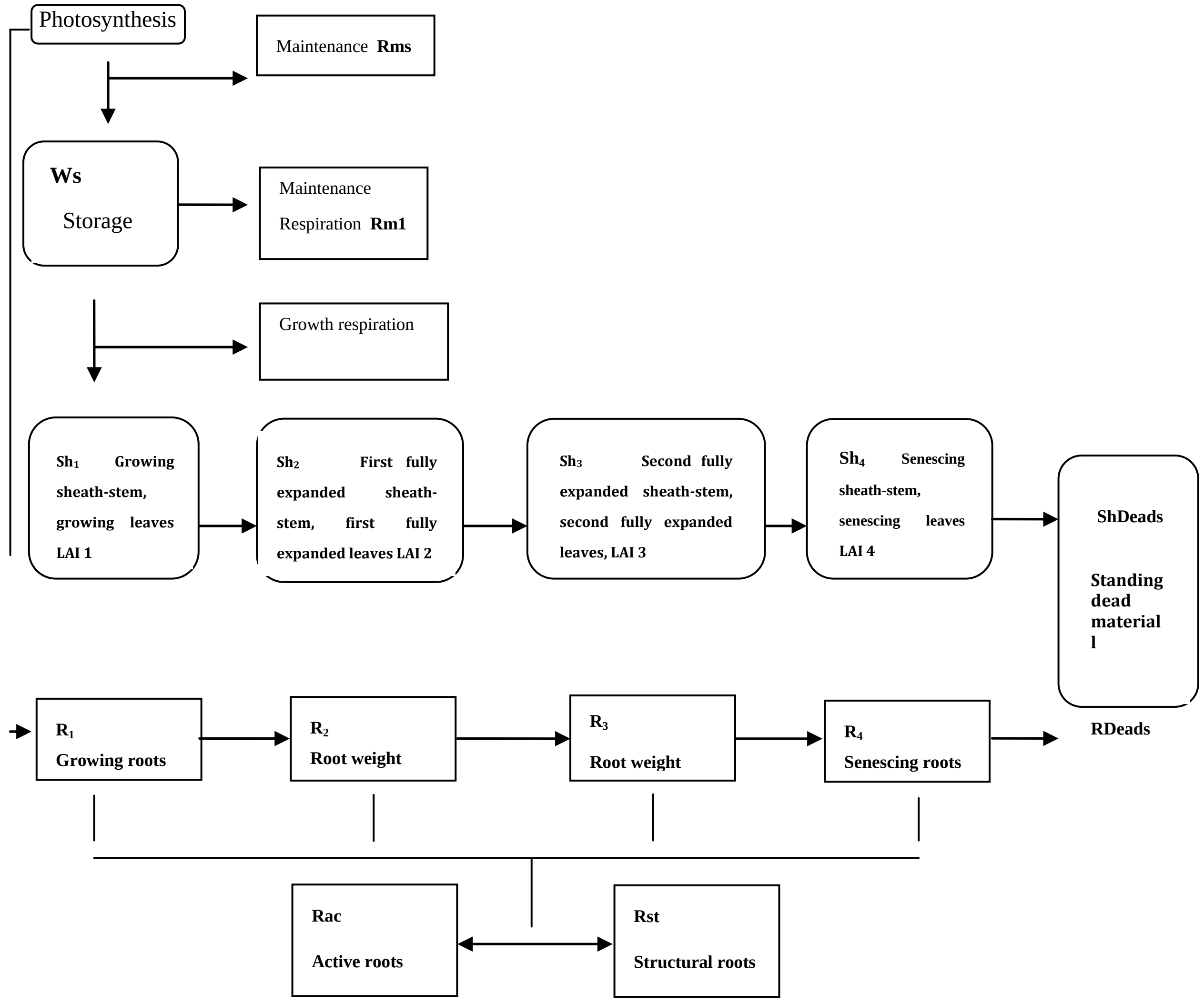

Fig. 1. Schematic representation of the Star grass model, as modified from Johnson and Thornley (1983) and Silveira (1999).

General structure of the submodel

The SG model requires a minimum soil temperature and soil moisture content to initiate re-growth. Thus, average soil temperature over the previous ten days (**T10**) must be higher than the minimum threshold temperature (**T_{min}**=11°C) and lower than the maximum threshold temperature (**T_{max}**=45° C). The superficial soil moisture (**MSoilsup**) must be greater than the drought tolerance coefficient (**DTC**). DTC is 0.5 for most C4 plants (Ngijyen 2005). Therefore, re-growth begins after the following conditions are met:

$$T_{min} < T10 < T_{max}. \quad (1)$$

$$MSoilsup > \mathrm{DTC}. \quad (2)$$

The live structural shoot (***Sh***) and root (***R***) dry matter weight (g m^{-2}) comprise four age categories, as in Thornley and Verberne (1989) (Figure 1): $Wsh._i$, $Wr._i$, i=1,2,3,4; the shoot and root structural dry matter, ***Sh***, ***R*** are:

$$Sh = Sh_1 + Sh_2 + Sh_3 + Sh_4$$

$$R = R_1 + R_2 + R_3 + R_4 \quad (3)$$

The total live structural dry matter (**SDM**) is (g structural dry weight m^{-2}):

$$SDM = Sh + R \quad (4)$$

The total leaf area index (**SLAI**) is divided similarly into four live structural leaf compartments:

$$SLAI = LAI_1 + LAI_2 + LAI_3 + LAI_4 \quad (5)$$

The shoot dry matter components are subdivided into lamina (**Leaff**) and sheath-stem (**Stem**), and comprise four age categories, as in Thornley and Verberne (1989). As mentioned earlier, roots were split into two types, structural and active. The response to deficiencies in soil-based resources exerts a change in the pattern of growth, favoring root growth over shoot growth. However, increased root growth will not necessarily result in increased nutrient uptake, and hence in alleviation of the deficiency. Since nutrient uptake depends to a greater extent on the geometry of the root system, the greatest return on this investment will be achieved if root length is maximized. This implies that the production of fine roots will be favored, since they achieve the greatest root length for a given weight (Fitter 1997). Therefore, in the SG model the active roots (**Rac**) (g m^{-2}) represent the thinner roots (feeder roots), while structural roots (**Rst**) (g m^{-2}) represent the thicker roots. These types of roots influence the rates of mineral uptake. The roots dry matter (**R$_o$**) are (g m^{-2}):

$$R_o=\sum^{4}_{i=1}(Rac_i + Rst_i) \quad (6)$$

In addition to these original live compartments, a stand dead compartment (**ShDead**) (g m^{-2}) and a roots dead compartment (**RDead**) (g m^{-2}) were added by Silveira (1999) to the original model constructed by Thornley and Verberne (1989) (Figure 1). These new compartments link the plant and soil models (not presented in this paper) in order to arrive at a better representation of senescence and recycling of nutrients, as will be described later in the senescence and recycling submodel section.

There are three plant substrates (g m^{-2}): substrate C (**SC**), substrate N (**SN**), and substrate P (**SP**). The SC is represented in the model by the following equation from Thornley and Verberne (1989):

$$\frac{\mathrm{dSC}}{\mathrm{dt}} = Cinput + SCS \text{ - } Rg\text{-}Rm\text{-}Rmu \quad (7)$$

where **Cinput** (g m^{-2}) is the daily carbon input from photosynthesis (Figure 1), and **SCS** (g m^{-2}) is the rate of C supply from recycling. The terms **Rg**, **Rm** and **Rmu** (g m^{-2}) represent the C loss by substrate pool to growth, maintenance and respiration associated with mineral uptake. The C loss associated with the reproductive stage was eliminated in the SG model because it does not simulate the reproduction process, and therefore no C has been allocated to seed production. The plant emergence subroutine described in Silveira's (1999) model was also eliminated because Star grass is propagated by stolons and it was assumed that the plants remain in a vegetative stage. Authors acknowledge that the star grass plant produces seed throughout the year, however it does not play an important role in the propagation of the plant and in modeling terms it would had added a complex subroutine with little application in practical terms, thus it was decided to leave seed production out the model. The model assumes that during the first days before **Sh** appears, plant maintenance is obtained from the root's soluble carbon (**SC**) (**R**) (Silveira 1999). This process is represented by:

$$\frac{\mathrm{dSC}}{\mathrm{dt}} = Cinput + \left(CGMax\right) \quad (8)$$

CGMax (g m^{-2}) is obtained by:

$$CGMax = 0.2\ FC \quad (9)$$

FC (g C (g structure)$^{-1}$) is the parameter fraction of C in the plant structure. The value 0.2 is the numerical assumption obtained from Johnson (1985). In optimum conditions 16% of FC in the plant could be assumed as soluble.

The substrate N (**SN**) (g m^{-2}) is calculated by:

$$\frac{\mathrm{dSN}}{\mathrm{dt}} = \mathrm{Nu} + \mathrm{SNS} \text{ - } (\mathrm{FN} \times (GSh + GR)) \quad (10)$$

The daily amount of nitrogen uptake (**Nu**) (g m^{-2}) and the rate of supply from senescence (**SNS**) (g m^{-2}) are the inputs to the substrate pool. The fraction of N (g N (g structure)$^{-1}$) in the live plant structure (**FN**) utilized in the synthesis of new shoot (**Sh**) and root (**R**) (g m^{-2}) represents the N loss from the pool. As in the C subroutine, the translocation of N to seed was eliminated.

The same assumption for C is made for N after the re-growing. Consequently, the **SN** (g m^{-2}) during this time is represented by Silveira (1999) as follows:

$$\mathrm{NGMax} = 0.5\,FN \quad (11)$$

$$\frac{\mathrm{dSN}}{\mathrm{dt}} = \mathrm{Nu} + \left(NGMax\right) \quad (12)$$

Johnson (1985) contemplated 33% as an optimum value for soluble N in the total plant N. Therefore, the

N soluble can be calculated as 50% of plant structural N that corresponds to 33% of N.

The subroutine for P substrate follows the same approach as for C and N. The total storage dry matter (**TSDM**) (g structural dry weight m^{-2}) in the Star grass model is represented in the same way as in Thornley and Verberne (1989):

$$\mathrm{TSDM} = \frac{MC}{12} SC + \frac{MN}{14} SN + \frac{MP}{32} SP \qquad (13)$$

where **MC**, **MN** and **MP** are the molecular masses of the C, N and P substrates relative to ^{12}C, ^{14}N and ^{32}P, respectively. The C, N and P substrate concentrations (**C**, **N** and **P**) are:

$$C = \frac{SC}{SDM} \qquad (14)$$

$$N = \frac{SN}{SDM} \qquad P = \frac{SP}{SDM}$$

SDM (g structural dry weight m^{-2}) is the total live structural plant. The fractions of the structural dry matter in the shoot (**FSh**) and root (**FR**) are:

$$FSh = \frac{Sh}{SDM} \qquad FR = \frac{R}{SDM} \qquad (15)$$

Assuming that the substrates are uniformly distributed, **FSh** and **FR** also describe the fractions of the total dry matter in the shoot and root. The total dry matter values of the shoot (**ShTot**), root (**RTot**) and plant (**Tot**) are (g structural dry weight m^{-2}):

$$\mathrm{ShTot} = Sh + FSh\,\mathrm{TSDM}$$

$$\mathrm{RTot} = R + \mathrm{FR\ TSDM}$$

$$\mathrm{Tot} = ShT + \mathrm{RTot} \qquad (16)$$

The total C, N and P concentrations in the live plant material are:

$$CPlant = \frac{SC + FC\ SDM}{Tot} \qquad NPlant = \frac{SN + FN\ SDM}{Tot} \qquad NPlant\ \frac{SP + FP\ SDM}{Tot} \qquad (17)$$

Growth and partition of nutrients

The rates of synthesis of new structural dry matter (g m^{-2}) in shoot (**GSh**) and root (**GR**) are given by Johnson and Thornley (1987):

$$GSh = Gc\ CN\ P\gamma ch\ Sh$$

$$GR = Gc\ C\ N\ P\ \gamma R\ R \qquad (18)$$

The growth coefficient (Gc) is obtained from Johnson (1985), amended by Silveira (1999), with the latter including a new coefficient for P in addition to the existing coefficients for C and N substrates:

$$Gc = \frac{PGR}{0.5\ CGMax\, NGMax\ PGMax} \qquad (19)$$

PGR is the potential growth rate(g m^{-2}), and **CGMax**, **NGMax** and **PGMax** are the optimum substrate concentrations at the potential growth rate (g m^{-2}). The potential growth rate for seeding plants is represented in the Star grass model as follows:

$$PGR = SGR \qquad (20)$$

SGR is the maximum growth rate (g m^{-2}). In equation 18, **γShs** and **γRs** are dimension-less functions that determine the relative partitioning between shoot and root. It is assumed that, $\gamma Sh + \gamma R = 1$. γSh and γR are determined in relation to the partitioning function (**PT**) described by Johnson and Thornley (1987):

$$\gamma Sh = \frac{PT}{1 + PT} \qquad (21)$$

$$\gamma R = 1/(1 + PT)$$

The model uses a teleonomically determined partitioning function that leads to maximum growth rate, considering two root functions (N and P), following Johnson and Thornley (1987):

$$\mathrm{PT} = \frac{\mathrm{FR}}{\mathrm{FSh}} \times \frac{\left[(\mathrm{N} + FN)/\mathrm{N} + (\mathrm{P} + FP)/\mathrm{P}\right]^{-1}}{\mathrm{C}(\mathrm{C} + FC)} \qquad (22)$$

One of the main contributions of the present work to the general structure of the original model constructed by Thornley and Verberne (1989) is made in the model's root structure. The partitions of roots between structural and active roots play an important role in simulating plant adaptation to the soil environment. The use of the same teleonomic approach, used by Thornley and Verbene (1989), simulates allocation of nutrients to shoots and roots and captures soil environment deficiency. The partition between structural and active roots is directly linked to **γR**. When there is a mineral deficiency in the soil, γR will be greater and active roots will grow more actively. In contrast, in a soil with a richer mineral environment, γR will be small and more structural roots will grow.

Leaf area index

New structural shoot growth (**GSh**) produces new lamina (g m^{-2}), or new sheath plus stem. Thus, the rate of production of new leaf area (**GLAI**) may be expressed, as in Johnson and Thornley (1985), as:

$$GLAI = \eta \, \mathrm{Flam} \, GSh \qquad (23)$$

Flam is a fraction of new shoot growth partitioned to lamina. $\boldsymbol{\eta_s}$ is the incremental specific leaf area (m^2 per grams of structure) and is defined by Johnson and Thornley (1985) as:

$$\eta_s = \eta m(1 - \zeta C) \qquad (24)$$

where **ηm** is the maximum value of the incremental specific leaf area and **ζ** is the incremental specific leaf area parameter.

Substrate utilization and respiration

The growth rate of new shoot structure (g m^{-2}) is **GSh** plus **GR**, which requires fluxes of C, N and P from the respective substrate pools. C can be lost by respiration associated with growth, maintenance and mineral uptake. C loss subroutines associated with growth and respiration can be seen in Thornley and Verberne (1989). Silveira (1999) introduced a new subroutine to deal with

C loss associated with respiration costs of N and P uptake (**RMu**) (g m^{-2}). It was used in the present model and is represented by:

$$RMu = \alpha M \, (\mathrm{Nu} + \mathrm{Pu}) \qquad (25)$$

The parameter **αM** represents the respiratory costs of mineral uptake. **Nu** and **Pu** are the daily amount of N and P uptake.

Fluxes between age categories

The fluxes of plant structure between the compartments are associated with a temperature-dependent rate parameter, **γSh$_\mathbf{i}$** in shoots and **γR$_\mathbf{i}$** in roots. Therefore,

$$\begin{aligned} &R_1 \rightarrow R_2\text{: } 2\,\gamma\; 2\,\gamma R\; c_1 \quad , \quad 2\,\gamma 2_s\; RSt_1 \\ &R_2 \rightarrow R_3\text{: } \gamma \;\; \gamma R \quad _2 \quad , \quad \gamma \quad _s\; RSt_2 \\ &Rt_3 \rightarrow R_4\text{: } \gamma\; \gamma R \;\; R \;\; _3 \quad , \quad \gamma \quad _s\; RSt_3 \end{aligned} \qquad (26)$$

$$\begin{aligned} &Sh_1 \rightarrow Sh_2\text{: } 2\,\gamma\; 2\,\gamma S\, af_1, \quad 2\gamma \quad tem_1 \\ &Sh_2 \rightarrow Sh_3\text{: } \gamma \;\; \gamma Sh \;\; f_2 \quad , \;\; \gamma \quad Stem_2 \\ &Sh_3 \rightarrow Sh_4\text{: } \gamma \;\; \gamma Sh \;\; f_2 \quad , \;\; \gamma \quad Stem_3 \end{aligned} \qquad (27)$$

Note that Silveira's (1999) model adds a new subroutine (equation 37) to the Thornley and Verberne (1989) model, in order to account for the different types of roots, specifically structural (**Rst**) and active (**Rac**) roots. The factor of 2 in equation 37 (**RC**) arise because the weight of the average leaf and root passing from compartments 1 to 2 is approximately twice the weight of the average for the first compartment (Thornley and Verberne, 1989).

After the plant emerges, when the seed phytomass is allocated in the first shoot and root compartment, the fluxes between compartments are altered. This happens because the new plant has only growing leaves (first compartment), and consequently the second, third and four compartments are empty. Therefore, the flow between the first and second compartments initiates when the number of days after emergence meets the variable time to end leaf as growing leaf (**TEFL**). The same procedure is adopted to start the flux between the second and third compartments, when the number of days meet the variable time to end leaf as first fully expanded leaf (**TESL**). The same procedure is followed for the flows between the third and fourth compartments and to the flow out of the fourth compartment. Therefore,

$$\begin{aligned} TE_1L &= \frac{1}{\gamma Sh} \\ TE_2L &= 2\frac{1}{\gamma Sh} \\ TE_3L &= 3\frac{1}{\gamma Sh} \\ TE_4L &= 4\frac{1}{\gamma Sh} \end{aligned} \qquad (28)$$

The same procedure is followed for the below-ground compartments:

$$TE_4R = \frac{1}{\gamma R} \tag{29}$$

$$TE_2R = 2\frac{1}{\gamma R}$$

$$TE_3R = 3\frac{1}{\gamma R}$$

$$TE_4R = 4\frac{1}{\gamma R}$$

The fluxes between aerial compartments may also be modified due to frost stress, harvest or animal breakdown.

Photosynthesis submodel

Diverse models of photosynthesis are available in the literature, separately or as part of plant models with different degrees of complexity (Detling *et a.,l* 1979; Monteith 1981; Johnson and Thornley, 1983, 1984; Rimmington, 1984; Johnson *et al*., 1989; Hanson 1991; Johnson *et al*., 1995). The photosynthesis submodel used in the present SG model is based on the photosynthesis model used by Johnson and Thornley (1984), which considers only irradiance and temperature effects on leaf photosynthesis. Modifications were made, however, in weight units from kilogram to gram and with the inclusion of a different approach to the temperature effect. The approach used to simulate the effect of temperature was modified from the linear effect adapted by Johnson and Thornley (1984) to a bell function following the Hanson *et al.* (1988) approach. Water stress was also included as a factor to reduce the photosynthesis rate. As in Silveira (1999), competition for light was not considered in the model due to the relative homogeneous leaf distribution in the pasture canopy that is managed by grazing or frequent cutting (Hanson *et al*. 1988, Thornley and Johnson 1990).

The single leaf gross photosynthetic rate (**PLg**) is found by the lower root of a non-rectangular hyperbola, which is:

$$\mathrm{PLg} = \frac{1}{2}\left[\alpha \mathrm{I} + Pm - \left\{\left(\alpha + Pm\right)^2 - 4\theta\alpha\, \mathrm{I}Pm\right\}^{1/2}\right] \tag{30}$$

I is irradiance (W/m^2) in photosynthetic active radiation (**PAR**). α and θ are the leaf photochemical efficiency (g CO^2 J^{-1}) and single leaf photosynthesis, respectively. The light saturated leaf gross photosynthetic rate (g CO^2 m^2 (leaf)/sec.), which is temperature dependent, is calculated by:

$$Pm = Polm * ETPP \tag{31}$$

Polm is the optimum light leaf gross photosynthetic rate (g CO^2 /m^2 (leaf)/sec.). The effect of temperature on plant processes (**ETPP**) is represented by a Gaussian function, following Hanson *et al*. (1988):

$$ETPP = \left[\left[\frac{\mathrm{MaxT} - \mathrm{TMean}}{\mathrm{MaxT\,OptT}}\right]\left[\frac{\mathrm{TMean} - \mathrm{MinT}}{\mathrm{OptT} - \mathrm{MinT}}\right]^{\frac{\mathbf{OptT - MinT}}{\mathbf{MaxT - OptT}}}\right]^{\mathrm{Z}} \tag{32}$$

MaxT, **MinT** and **OptT** are the maximum, minimum and optimum temperatures for positive plant activity (^{o}C). **TMean** is the mean daily temperature (^{o}C), and Z is the shape parameter for the curve.

The Gaussian function was chosen because physiological processes in plants normally have an optimum temperature, and consequently temperatures below or above this point depress plant activity (Hanson *et al*. 1988, Mooney and Ehleringer 1997). In the case of the SG, these temperatures are MaxT= 45 ^{o}C, MinT= 11 ^{o}C and OpT= 30^{o}C. The ascending arm of the curve represents a temperature-dependent stimulation of photosynthesis up to an optimum level; the descending arm is associated with deleterious effects, some of which are reversible while others are not (Taiz and Zeiger 1991). Thus, the bell function is considered to be better than a linear equation in representing the effect of temperature in plant behavior. This equation is adopted in the SG model for all processes in plants that are affected by temperature.

The effective C available for plant growth can be limited by water plant stress. The effect of water on plant processes is represented in different models throughout a scalar effect (0-1). The ratio of the actual to potential transpiration is used by Verberne (1992) and Moore *et al*. (1997), while Hanson *et al*. (1988) used the water potential to establish this relation. The SG model uses water content in the soil (**MSoilTot**) in relation to field capacity (**Wfc**) and wilting point (**Wwp**) from the water submodel to establish soil moisture. This ratio is considered in the SG model to simulate the effect of soil moisture on plant processes (**ESMPP**) as follows:

$$ESMPP = \frac{\dfrac{MSoilTot\text{-}Wwp}{Wfc\text{-}Wwp}}{DTC} \tag{33}$$

The drought tolerance coefficient (**DTC**) parameter determines the minimum level of soil moisture at which plant processes are not affected. In the case of SG, the DTC is 0.5, and from this point, the model assumes the reduction of soil moisture as a linear scalar effect until the wilting point.

Mineral uptake submodel

In the mineral uptake submodel, soil conditions follow the approach of root activity in the nutrient depletion zone. Nitrate is readily soluble and highly mobile in the soil, while phosphorus is less soluble and relatively immobile (Hopkins 1995). This is considered in the model through the parameters for minimum N soil (**MNSoil**) and minimum P soil (**MPSoil**).

NGMax plus the amount of structural N needed for maximum daily growth are assumed to be the potential N uptake per gram of roots (**PNUGR**) in an optimum environment. **PGR** is the potential daily growth rate (Silveira 1999).

$$\mathrm{PNUGR} = \mathrm{NGMax} + PGR * FN \qquad (34)$$

In order to become quantitative, the theoretical approach proposed by Tilman (1997) is used to express the effect of N in the soil (**ENSoil**):

$$ENSoil = \frac{\mathrm{NAPL}}{MNSoil} \qquad (35)$$

NAPL is the amount of N in the soil that is obtained from the soil submodel. The **MNSoil** is a parameter that represents the minimum amount of N in the soil when the flow of mineral to the nutrient depletion zone is not affected.

The model assumes a scalar effect of plant nitrogen (**ENplant**) that is represented in Silveira's model (1999) as:

$$ENplant = \frac{NGMax + FN - NPlant}{\frac{NGMax}{2}} \qquad (36)$$

NGMax is the maximum soluble N in a plant and **NPlant** is the total N concentration in a live plant (**CPlant**, **NPlant**, **PPlant**). The parameter FN is the fraction of N in a structural plant. Therefore, the model assumes there is a maximum level of soluble nitrogen in a plant (Johnson 1985, Murtagh *et al.* 1990) above which nitrogen uptake ceases. In addition, it is assumed that there is a linear depressive effect in the nitrogen uptake from this limit to 50% of the limit.

The model's active roots are considered to be one hundred percent capable of uptaking N and P, with the exception of **Rac$_4$** when the uptake efficiency of the fourth compartment is assumed to be half of the others because of the senescent stage of the roots. However, structural roots are considered to have half the capability of active roots to uptake minerals due to their thickness. Therefore, root capability (**RC**) according to Silveira (1999) is:

$$\begin{aligned}\mathrm{RC} &= Rac_1 + Rac_2 2 + Rac_3 + Rac_4\ \ 0.5 + \\ &(Rst_1 + Rst_2 + Rst_3)0.5 + Rst_4\ \ 0.25 \qquad (37)\end{aligned}$$

And thus, the potential N uptake (**PNU**) by roots is:

$$PNU = RC\ \ PNUGR\ \ \ ENSoil\ \ \ ENPlant \qquad (38)$$

Finally, abiotic factors must be considered, and consequently the effective amount of nitrogen uptake by a plant (**Nus**) is calculated after adjusting for temperature and moisture effects:

$$\mathrm{Nu} = PNu\ ETPP\ ESMPP \qquad (39)$$

Phosphorus uptake by a plant is simulated in the same way as nitrogen uptake, but the symbiotic association between fungus (mycorrhizae) and roots is also considered. The mycorrhizal-enhanced plant growth appears to be associated with a more efficient uptake of nutrients, especially phosphorus in impoverished soil (White 1987; Hopkins 1995). Mycorrhizal association increases the roots' area of contact with the soil, and therefore infected roots can transport phosphate at a rate more than four times higher than that of an uninfected root (Taiz and Zeiger 1991). In the model, the mycorrhizal effect (**Meff**) is simulated as a linear effect in accordance with the phosphorus available to the plant in the soil (**PApl**).

$$\begin{aligned}&\mathrm{Meff} = 4 - (1.5\,\mathrm{PApl}) && \mathrm{PApl} <= 2 \\ &\qquad\qquad\qquad \text{if} \\ &\mathrm{Meff} = 1 && \mathrm{PApl} > 2\end{aligned} \qquad (40)$$

In this way, the model behaves similarly to the model proposed by Rowel (1994), or in other words, in soil with large concentrations of available phosphorus, mycorrhizae do not increase uptake, because the root demand is easily satisfied by diffusion. The others equations to simulate phosphorus uptake follow the same approach as for nitrogen uptake, with only a change of symbol (N for P) in the name of the variable or parameter (e.g. Nu by Pu).

Ontogenic submodel

In the model developed by Silveira (1999), the ontogenic submodel of plant growth is represented in four stages: stage 1 is from germination to emergence, stage 2 is the vegetative period, stage 3 is the reproductive period before flowering, stage 4 is reproductive seed maturity, and stage 5 is senescence or dormancy. As mentioned earlier, the reproductive phase is not simulated in the present SG model.

Senescence and recycling submodel

The senescence and recycling submodel was developed to make the link between plant and soil models. It considers the recycling simulation processes described by Thornley and Verbene (1989) and the individual mineral inputs required by the Century model (Parton *et al*., 1987) to simulate plant litter degradation. The fluxes out of the fourth leaf and stem compartments ($FOLeaf_4$; $FOStem_4$) and the flux out of the fourth root active and structural compartments ($FORAc_4$; $FORSt_4$) are simulated according to the approach proposed by Silveira (1999):

$$
\begin{aligned}
FOLeaf_4 &= \gamma\ \gamma Sh\ Le_4 \\
FOStem_4 &= \gamma\ \gamma Sh\ St\ _4 \\
FORAc_4 &= \gamma\ \gamma R\ R\ _4 \\
FORSt_4 &= \gamma\ \gamma R\ R_4
\end{aligned}
\tag{41}
$$

$$
\begin{aligned}
FOLeaf_4 &= \gamma\ \gamma Sh\ Le_4 \\
FOStem_4 &= \gamma\ \gamma Sh\ St\ _4 \\
FORAc_4 &= \gamma\ \gamma R\ R\ _4 \\
FORSt_4 &= \gamma\ \gamma R\ R_4
\end{aligned}
$$

Therefore, the total flux out of shoot ($FOSh_4$) and root (FOR_4) live compartments are:

$$
\begin{aligned}
FOSh_4 &= FOLeaf_4 + FOStem_4 \\
FOR_4 &= FOAc_4 + FOSt_4
\end{aligned}
\tag{42}
$$

It is assumed that there is no loss of substrate C, N or P with these fluxes, but some structural C, N and P could be returned to the respective substrate pool, thereby simulating recycling of nutrients in the plant. The amount of recycled N and P depends on the substrate concentration, and C is assumed to be associated with N recycling. The parameters' value for structural degradation of N and P (**SdN**$_i$; **SdP**$_i$) and the substrate concentration determine the recyclable fraction of N (ϕ **N**) and P (ϕ **P**), so that:

N= SdN/(N+SdN)

$$\emptyset P = SdP/(P+SdP) \tag{43}$$

Thus, according to Moore *et al.* (1997), the amount of N supplied from recycled shoots (**SNSSh** and roots (**SNSR**) can be expressed as:

$$
\begin{aligned}
SNSSh &= \varphi NFNR\frac{FN}{FNR}FOSh_4 \\
SNSSh &= \emptyset NFMR\,\frac{FN}{FNR}\,FOR_4
\end{aligned}
\tag{44}
$$

FNR is the nitrogen fraction in the degradable structure. As with N, the amounts of P supplied from recycled shoots (**SPSSh**) and roots (**SPSR**) are:

$$SPSSh = \varphi PFPR\frac{FP}{FPR}FO\mathrm{Sh}_4 \tag{45}$$

$$SPSR = \varphi PFPR\,\frac{FP}{FPR}FOR_4$$

As in Moore *et al.* (1997), the amounts of C recycled from shoots (**SCSSh**$_i$) and roots (**SCSR**$_s$) are:

$$
\begin{aligned}
SCSR &= \varphi N\,FCR\,\frac{FN}{FNR}\;FOR_4 \\
SCSShs &= \varphi N\ FCR\frac{FN}{FNR}\;FOSh_4
\end{aligned}
\tag{46}
$$

The rates of supply of C, N and P from senescence (**SCS**$_i$;**SNS**$_s$ and **SPS**$_s$) are simulated by (Silveira 1999):

$$
\begin{aligned}
SPS &= SPSh + SPSR \\
SCS &= SCSh + SCSR \\
SNS &= SNSh + SNSR
\end{aligned}
\tag{47}
$$

To make the link between the plant and the soil models, the attached shoot and root compartment were divided by each element of the model. Therefore, C, N and P have a dead shoot and dead root compartment. The individual dead shoot compartments for each element (**ShDC**; **ShDN** and **ShDP**) are, respectively,

$$
\begin{aligned}
RDN &= FNDR - (\mathrm{RDN\,Decay\,R}) \\
ShDC &= FCDSh - (\mathrm{ShDC\,Decay\,Sh}) \\
ShDP &= FPDSh - (\mathrm{ShDP\,Decay\,Sh}) \\
ShDN &= FNDSh - (ShDN\ \mathrm{Decay\,Sh})
\end{aligned}
\tag{48}
$$

In the same way, the dead roots compartments (**RDC**; **RDN** and **RDP**) are:

$$RDC = FCDR - \left(RDC \ \mathrm{DecayR}\right)$$
$$RDP = FPDR - \left(RDP \ \mathrm{DecayR}\right) \qquad (49)$$

DecaySh and DecayR are the parameters that represent the decay rate from dead shoots and roots to litter in the soil. The **FCDSH**, **FNDSH** and **FPDSH** are the flow of C, N and P from live shoot to dead shoot pools:

$$\mathrm{FCDSh} = (FC \ \mathrm{FOSh_4}) - \mathrm{SCSSh}$$
$$\mathrm{FPDSh} = (FP \ \mathrm{FOSh_4}) - \mathrm{SPSSh}$$
$$\mathrm{FNDSh} = (FN \ \mathrm{FOSh_4}) - \mathrm{SNSSh} \qquad (50)$$

The flows to dead roots (**FCDR**; **FNDR**; **FPDR**) are represented by:

$$FCDR = (\mathrm{FC \ FOR_4}) - SCSR \qquad (51)$$
$$FPDR = (\mathrm{FP} \ FOR_4) - SPSR$$
$$FNDR = (\mathrm{FN} \ FOR_4) - SNSR$$

The shoot dead pool (**ShDead**) is calculated by:

$$\mathrm{ShDead} = \mathrm{FOSh_4} - \left(\mathrm{ShDead} \ DecaySh\right) \qquad (52)$$

In the same way, to link the plant and animal models, the SG simulates the fractions of C, N and P in the dead shoot material:

$$\mathrm{FCShD} = \frac{ShDC}{\mathrm{ShDead}}$$
$$\mathrm{FNShD} = \frac{ShDN}{\mathrm{ShDead}} \qquad (53)$$
$$\mathrm{FPShD} = \frac{ShDP}{\mathrm{ShDead}}$$

The amount of N in the surface and root litter (**Nsl;Nrl**) is represented by:

$$\mathrm{Nsl} = \sum_{i=1}^{s} \left(\mathrm{ShDN} \, DecaySh\right)_i$$
$$\mathrm{Nrl} = \sum_{i=1}^{s} \left(\mathrm{RDN} \, DecayR\right)_i \qquad (54)$$

And P (**Psl**;**Prl**) is represented by:

$$\mathrm{Prl} = \sum_{i=1}^{s} \left(\mathrm{RDP} \, DecayR\right)_i \qquad (55)$$
$$\mathrm{Psl} = \sum_{i=1}^{s} \left(\mathrm{ShDP} \, DecaySh\right)_i$$

C is split into a lignin and C fraction:

$$\mathrm{Crl} = \sum_{i=1}^{s} \left(\left(1 - \mathrm{Plig}\right) \mathrm{RDC} \ DecayR_s\right)_i \qquad (56)$$
$$C\mathrm{sl} = \sum_{i=1}^{s} \left(\left(1 - \mathrm{Plig}\right) \mathrm{ShDC} \ DecaySh\right)_i$$

The fraction of lignin (**Lrl**;**Lsl**) is represented by:

$$\mathrm{Lrl} = \sum_{i=1}^{s} \left(\mathrm{Plig} \, \mathrm{RDC} \ DecayR\right)_i \qquad (57)$$
$$\mathrm{Lsl} = \sum_{i=1}^{s} \left(\mathrm{Plig} \, \mathrm{ShDC} \ DecaySh\right)_i$$

The percentage of lignin (**Plig**) is obtained by:

$$Plig = \frac{Flplants}{FC} \qquad (58)$$

where the parameter value for the fraction of lignin in the plant (**Flplant**$_s$) is ontogenic-dependent.

$$\begin{array}{lll} \mathrm{LeafRe}_4 = 1 & & \mathrm{ShHarv} < 50 \\ \mathrm{LeafRe}_4 = 1.2 - .004\,\mathrm{ShHarv} & \text{if} & \mathrm{ShHarv} \ge 50 \text{ and } \le 200 \\ \mathrm{LeafRe}_4 = 0.4 & & \mathrm{ShHarv} > 200 \end{array}$$

Disturbances submodel

Two types of disturbances are contemplated in the SG: natural disturbances and human disturbances. Drought is considered to be a natural disturbance, while harvest or cutting, fire and grazing by large mammals are considered to be human influences that can modify plant processes. The effect of drought is simulated through the effect of soil moisture on plant processes (ESMPP), as described in the photosynthesis section. In Silveira's original model (1999), frost is considered to be a natural disturbance, but it was not included in the present model because frost is absent in tropical climate regions.

Fire

A plant is considered to be dead when fire occurs. Therefore, all live and dead compartments above-ground of plants are considered empty and the minerals (N and P) go directly into the available plant mineral pool (**NApl** and **PApl**) in the soil submodel. The C, N and P present in the live compartments below ground are allocated to the corresponding dead root compartments, **RDC**, **RDN** and **RDP**.

Harvest or cutting

To calculate the dry matter yield from cutting, the increments in shoot structural dry matter are first calculated, and the harvestable dry weight (**HarvShs**) is obtained as proposed in Johnson and Thornley (1985):

$$\mathrm{HarvSh} = \mathrm{Sh} - \mathrm{Sh}\,(t-1) \qquad \text{if} \qquad \mathrm{Sh} - \mathrm{Sh}\,(t-1) > 0$$

$$\mathrm{HarvSh} = 0 \qquad \text{if} \qquad \mathrm{Sh} - \mathrm{Sh}\,(t-1) \le 0$$

(59)

The total harvestable dry weight (**ShHarv**) is then taken to be:

(60)

$$\mathrm{ShHarv} = \frac{\mathrm{ShTot} \times \sum_{i=1}^{s} \mathrm{Hsh}_i}{\mathrm{Sh}}$$

The effective shoot harvest (**EShHarvs**) at the moment of cutting must be related to the amount of forage that remains in the field. This is simulated by the proportion of material in the third and fourth leaf compartments that remains in the field (**LeafRe$_3$**; **LeafRe$_4$**).

Therefore, according to Silveira (1999): (61)

$$\mathrm{LeafRe}_3 = 1 - 0.017\,\mathrm{ShHarv} \qquad \mathrm{ShHarv} \le 50$$

if

$$\mathrm{LeafRe}_3 = 0.15 \qquad \mathrm{ShHarv} > 50$$

(62)

The same assumption was made for the third and fourth stem compartments that remain in the field (**StemReT**$_s$; **StemRe**$_{4s}$).

The percentage of harvestable forage that remains in the field will be higher when less forage is available to be harvested, mainly at low levels. Therefore, the model assumes that the effective harvest by plant or functional group (**EShHarv**) is simulated by:

$$\mathrm{EShHarv} = \mathrm{ShHarv} - \left(\mathrm{LeafReT} + \mathrm{StemReT} + \mathrm{LeafRe}_4 + \mathrm{StemRe}_4\right)\mathrm{ShT} \qquad (63)$$

And the total harvestable dry weight (**ShHarvTot**) is:

(64)

$$\mathrm{ShHarvTot} = \sum_{i=1}^{s} \mathrm{EShHarv}$$

After harvest or cutting, the model assumes that the first and second above-ground compartments are empty, so the flux between the two compartments and the flux between the second and third compartments of the model are altered. Consequently, the flows between compartments begin again when the number of days after harvest meets the TEFL$_s$ and TESL variables$_s$ respectively.

When whole-plant photosynthetic capacity is reduced by substantial defoliation, the effects of reduced carbon supply rapidly propagate through a growing plant, affecting shoot growth, root respiration, nutrient uptake and root growth (Richards 1993). These effects are simulated in the model as follows:

Flows between the third and fourth compartments and the flow out of the four compartments are double delayed, simulating the recover of leaf photosynthesis activity.

These two last effects cease when the C balance becomes positive. The C balance (**CBalances**) is simulated by:

$$\mathrm{CBalance} = \mathrm{Cinput} + \mathrm{SCS} - \mathrm{Rg} - \mathrm{Rm} - \mathrm{Rmu} \qquad (65)$$

Grazing

Grazing by cattle is simulated by the direct impact in the above-ground compartments. Each above-ground compartment (alive and dead) can give some contribution to the total daily animal intake. The amount of biomass of each compartment is defined in the animal submodel, not addressed in this paper. Therefore, the amount of biomass from each compartment consumed every day by an animal (e.g. intake of shoots from the first compartment, **Leaf$_1$** plus **Stem$_1$**) is subtracted from the biomass of these compartments (e.g. Leaf$_1$ and Stem$_1$). The amount of forage consumed by each head of cattle per day is restricted to 1% of their live weight, because it is assumed that they receive supplemental feed. So when the dry matter intake (kg DM day^{-1}) reaches 1% of their body weight the animal stops eating. The number of head of cattle per hectare is a parameter that is set by the model operator, because it depends on forrage availability.

The biomass trampled by livestock (**BTLs**) is represented in the model according to the approach by Hanson *et al*. (1988):

$$\mathrm{BTL} = \mathrm{Sh}(1 - \exp(-\mathrm{TSSR} * \mathrm{ASR})) \qquad (66)$$

TSSRs is the parameter tolerance to stocking rate as in Silveira (1999) and **ASR** is the animal stocking rate.

The effect on each compartment is proportional to compartment contribution to the total plant biomass. Therefore, the effect on the leaf first compartment (BTLeaffs) is simulated by:

$$BTLeaf_1 = \frac{Leaf_1}{Sh} BTL \qquad (67)$$

The same method is used to simulate the impact of trampling on the other above-ground compartments.

The amount of N, P and C present in the biomass trampled by livestock (BTLs) is directly added to the N, P and C in the surface litter (**Nsl**; **Psl**; **Csl** and **Lsl**, equations 54, 55, 56 and 57).

Summary of minimum data set used for the SG model development and validation

Data on SGused for our model development was gathered from the literature (Caro-Costas *et al*., 1976; layton and Harlan 1970; Gredpac 1990, Manson and Burton 1982; Ortega and Gonzalez 1990; Pozo *et al*., 2000; Porto *et al*. 2009), and from direct measurements on three paddocks comprised of Star grass, named A, B and C. The paddocks were located in the Tejupilco municipality in the southwest region of the State of Mexico, at 18º 45´30", 19º 04´32" North; 99º 59´ 07", 100º 36´ 45"West; at an altitude of 1,340 m. The predominant climate is warm sub-humid (A(C) w2 (w) (i') g) (Garcia, 1973).

Agronomic data collected from Star grass paddocks

Tree small-scale dairy farms were surveyed from April 2006 to May 2007, and three Star grass paddocks of 1 hectare each from these farms were used for this study (named A,B,C). The farmers used a continuous grazing system and the stocking rate varied according to the seasons, but three cows per hectare were grazing in the experimental paddocks on average.

The agronomic variables evaluated on each paddock included: forage availability (kg DM ha^{-1}), amount of live-dead grass material (kg DM ha^{-1}) and stem-leaf ratio. The techniques proposed by Hodgson (1994) were used to measure these variables. The agronomic variables and leaf area index were measured monthly over a period of one year, and the results for paddock A are shown in Figure 2 six exclusion cages per paddock were used to estimate forage accumulation and availability. In addition, SG forage samples were collected in order to determine the crude protein (CP) content, the monthly average CP concentration for the three experimental paddocks are shown in Table 1. The extinction coefficient necessary to calculate photosynthesis was estimated according to Ludlow (1985).

Leaf area index estimation

In experimental paddock A, an area of 37.5 m^2 was protected from cattle grazing with a fence. Then, all the grass within the protected area was cut at ground level and this was considered as day zero. Subsequently, ten plants within the protected area were marked with a permanent red mark in order to measure leaf growth rate and development every eight days during a total of 72 days. Leaf area index was then estimated for each leaf by measuring leaf length from the ligule to the apice, and leaf width measured at the middle point of the leaf with the use of a digital vernier. The leaf area index in relation to the number of leaves and the age of the plants is shown in Figure 3.

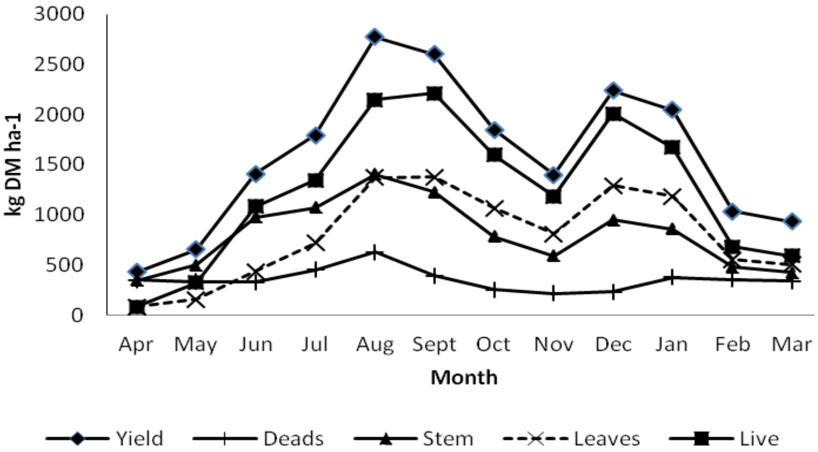

Figure 2. Agronomic sward variables measured monthly in the experimental Star grass paddock A used for model development.

Table 1. Monthly average Nitrogen and crude protein concentration of the three experimental paddocks planted with Star grass (, g kg^{-1} DM) in the municipality of Tejupilco, Mexico

Months	**N (g kg^{-1}DM)**	**Sd**	**CP (g kg^{-1} DM)**
April	4.81	0.32	30.1
May	10.95	0.32	68.4
June	22.29	0.47	139.3
July	22.55	0.50	140.9
August	20.36	0.14	127.3
September	17.68	1.59	110.5
October	15.47	0.64	96.7
November	13.59	0.43	84.9
December	13.49	1.54	84.3
January	9.83	0.16	61.4
February	8.73	0.33	54.6
March	5.30	0.02	33.1

Sd=Standard Deviation. CP=crude protein

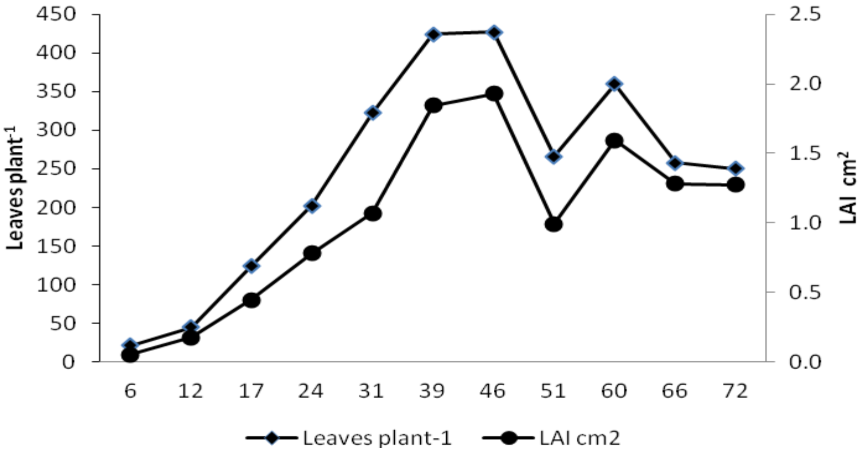

Figure 3. Behavior of the observed leaf area index (LAF) as affected by the age of the plant and number of leaves for the SG paddock A in the southwest region of the State of Mexico

Coefficient of extinction (k1)

Thes coefficient was not measured in the field, however there are reports of a range of 0.36 to 0.94 in tropical grasses. Ludlow (1985), for example, estimated a k1 value for Kikuyu grass (*Pennisetum clandestinum*) of 0.53 to 0.63. There were no k1 values found in the literature for SG and therefore in this study a value of 0.6 was used, since this value applies for most tropical grasses (Ludlow 1985).

Climate variables

Table 2 shows the average climate variables registered during the experimental period. Note that for model development daily climate data was used. Climate data was obtained from a climatic stations near the study area.

Table 2. Average annual climate conditions in the Tejupilco municipality in the southwest region of the State of Mexico

Variable	**Description**	**Value**
Rain	rainfall, mm day $^{-1}$	2.8
RH	relative humidity, %	64.2
Sun	bright sunshine hours per day, h	6.4
TMean	mean daily temperature, ^{o}C	20.8
TMax	maximum daily temperature, ^{o}C	27.7
TMin	minimum daily temperature, ^{o}C	14.9
T10	ten-day average air temperature, ^{o}C	20.8
Wind	mean wind speed at 2 m height, km h^{-1}	2.5

Source: Comisión Nacional del Agua. Delegación Estado de México.

Soil parameters

Soil samples were colleted in order to determine the soil characteristics in the paddocks that were used for model development and calibration. A random sampling was carried out at each of the three SG paddocks. Soil samples were collected every 20 cm up to a one-meter depth, and then all samples were mixed up and homogenized in order to get one sample for soil analysis. Results for soil analyses are shown in Table 3.

On average the soils of the experimental paddocks had 0.35 sand, 0.38 clay and 0.27 loam. The Century soil simulator (http://www.nrel.colostate.edu/projects/century/ accessed 20/01/2011) was used to estimate the wilting point (0.1780), field capacity (0.3623) and saturated hydraulic conductivity (0.0006). The drought tolerance coefficient (DTC) was lowered from 0.6 in C3 plants to 0.5 in C4 plants, since Star grass is more tolerant to drought periods (FAO, 2010) than temperate grass species.

Table 3. Physical and chemical characteristics of the soil at the experimental Star grass paddocks in the Tejupilco municipality in the southwest region of the State of Mexico

1

	Organic matter	pH	Ca (cmol/kg)	Mg (cmol/kg)	P (mg/ kg-1)	N (%)	Texture	Humidity (%)	Water-holding capacity (%)	Bulk density (g/cm3)	Organic carbon (%)	N
(0-20cm)	2.61	4.13	0.10	2.60	10.75	0.17	Sandy loam	14.23	51.66	1.17	4.49	3
(20-40cm)	1.52	4.32	1.35	2.55	8.62	0.10	Sandy	15.38	54.80	1.11	2.62	3
(40-60cm)	1.25	4.63	0.00	1.85	7.70	0.06	Clay loam	16.20	52.26	1.26	2.15	3
(60-80cm)	1.33	4.85	0.80	2.80	7.83	0.06	Clay loam	15.84	51.40	1.24	2.29	3
(80-100cm)	1.56	4.97	0.80	5.00	8.00	0.08	Clay loam	13.58	50.58	1.18	2.69	3

RESULTS

Comparison of model predictions for forage availability *vs* observations measured in experimental padocks

Dry matter availability data measured in experimental paddock A was used for validating the Star grass model's predictions. The confidence intervals for observed dry matter availability data were calculated as in Steel and Torrie (1980), and plotted against the model's predictions as shown in Figure 4. It can be seen that the model's prediction for dry matter availability values during most of the year fall within the confidence intervals of the observed data ($P<0.05$). The SG model is also capable of simulating the growth pattern of the SG throughout its growing cycle, as shown in Figure 4.

The observed and predicted data of forage availability for SG experimental paddock A in different harvest periods were also analyzed using regression analysis, as suggested by Tedeschi (2006), in order to determine the accuracy and precision of the model's predictions as seen in Figure 5. It can be observed that the predicted data were accurate because they were very close to the regression line (dotted line, $R^2=0.92$), and also precise because the two regression lines are almost overlapping.

Model validation

A minimum data set similar to that used to develop the SG model was collected in paddocks B and C. This data was inputted to the model, and plant growth and forage production were simulated and then compared using regression analysis with observed values. Figures 6 and 7 show the relationship between observed and simulated data for forage availability.Figures 6 and 7 show that the SG model is successful in simulating forage availability for paddocks B and C ($P<0.05$, $R^2=0.88$; $R^2=0.96$, respectively).

CONCLUSIONS

This study showed that it is possible to adapt a grass model developed for temperate climates in order to simulate growth and development of a tropical grass species. The model was accurate at simulating Star grass gowth for the particular conditions fo central Mexico. However, during the model development process it became evident that there is little information published on plant physiology for tropical grasses such as Star grass. Thus it is necessary to conduct more research in this area, particularly on the effect of the photoperiod on photosynthesis and the growth rate. There is also a need to generate more information on growth, development and response of Star grass to different climate and management conditions in the tropics, including irrigation, fertilization, stocking rates, and different grazing frequencies. After this information has been collected, it will be possible to challenge the Star grass model for different situations and generate alternative management scenarios.

Acknowledgments

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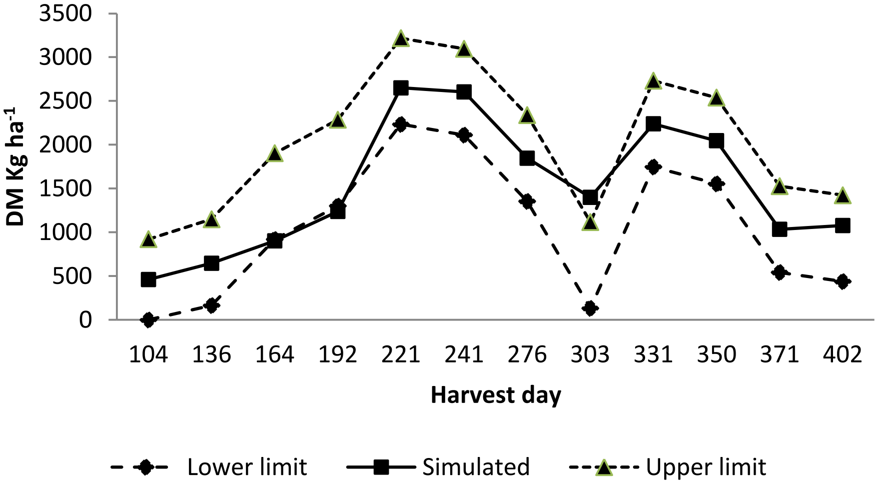

Figure 4. Comparison between the SG model's predictions with adjusted (95%) confidence intervals for dry matter yield observed for experimental paddock A during an annual growing cycle.

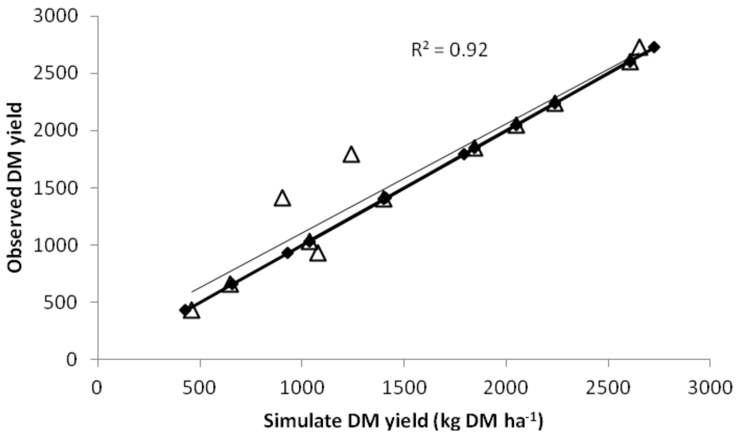

Figure 5. Accuracy and precision of the SG model predictions for DM availability, kg DM ha^{-1} (observed *vs* predicted regresion lines) for experimental paddock A.

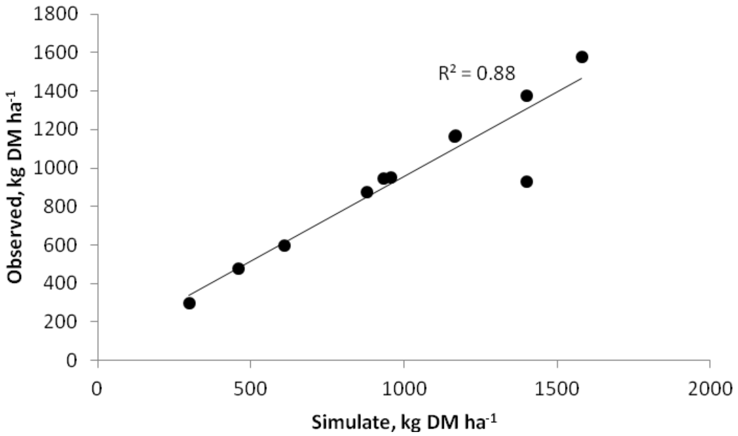

Figure 6. Observed *vs* predicted DM availability (kg DM ha^{-1}) for the experimental Star grass paddock B.

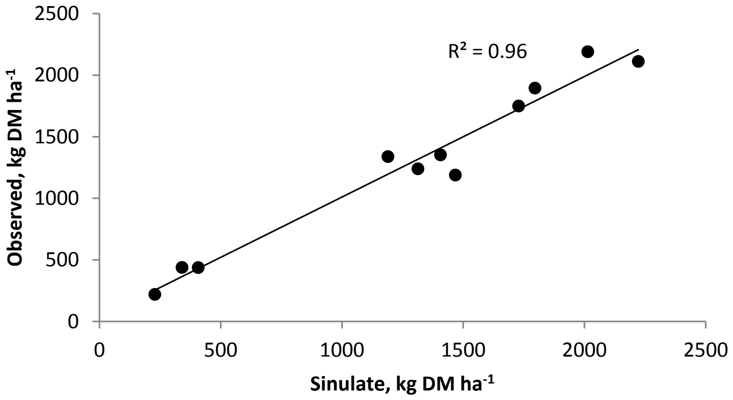

Figure 7. Observed *vs* predicted DM availability (kg DM ha^{-1}) for the experimental Star grass paddock C.

REFERENCES

Alocilja, E.C., & Ritchie, J.T. 198) Upland rice simulation and its use in multicriteria optimization. Michigan: IBSNAT.

Caro-Costas, R., F. Abruna, and J. Figerella. 1976. Effect of three levels of fertilization on the productivity of stargrass pastures growing on a steep ultisol in the humid mountain region of Puerto Rico. Exp. Stn., Univ. of Florida, Gainesville. J. Agric. Univ. PR 60:172–178.

Chaneton, E.J., Lemcoff, J.H. and Lavado, R.S., 1996 Nitrogen and phosphorus cycling in grazed and ungrazed plots in a temperate subhumid grassland in Argentina. Journal of Applied Ecology 33, 291-302.

Clayton, W.D. and Harlan, J.R., 1970 The genus Cynodon L.C. Rich in tropical Africa. Kew Bulletin, 24, 185–189.

Crawley, M.J., 1997 Life history and Environment. In: Crawley, M.J. (Ed.) Plant Ecology, pp. 73-131. Oxford: Blacwell Science.

Detling J.K., Parton W.J., & Hunt H.W., 1979. A simulation model of Boutelona gracilis biomass dynamics on the North American shortgrass prairie. Oecologia, 38, 167-191.

FAO. 2010. Cynodon plectostachyus (K. Schum.) Pilger. http://www.fao.org/ag/AGP /AGPC/doc/Gbase/DATA/PF000210.HTM accesado el 10 de diciembre 2010.

Fitter, A., 1997. Nutrient Acquisition. In: M.J. Crawley (Ed.), Plant Ecology. Oxford: Blacwell Science. pp. 51-72

Floate, M.J.S., 1970 Decomposition of organic materials from hill soils and pastures: II. The effect of temperature on the mineralization of carbon, nitrogen and phosphorus from plant materials and sheep faeces. Soil Biology Biochemical 2, 187-196.

García E., 1973. Modificaciones al sistema de clasificación climática de Kӧppen. 2.ed., Instituto de Geografía Universidad Nacional Autónoma de México

GREDPAC (Grupo regional de desarrollo de pastos y forrajes de Centroamerica, Mexico y el Caribe) 1990. Memoria. Cuarta reunión de consulta, Consulta, Ciego de Avila, Cuba. Octubre 1990. La Habana, Cuba, 172p.

Hanson J.D., Skiles J.W. and Parton W.J., 1988 A multi-species model for rangeland plant communities. Ecological Modelling 44, 89-123.

Hanson J.D., 1991Analytical solution of the rectangular hyperbola for estimating daily net photosynthesis. Ecological Modelling 58, 209-216.

Hodgson, J. , 1994. Manejo de pastos. Teoría y Práctica. Diana. México.

Herrero, M., Fawcett, R.H., Silveira V. , Busqué J., Bernué s A., Dent, J.B., 2000. Modelling the growth and utilisation of kikuyu grass *(Pennisetum clandestinum*) under grazing. 1. Model definition and parameterisation Agricultural Systems 65, 73-97.

Hopkins, W.G., 1995 Introduction to plant physiology. New York: John Wiley & Sons, Inc.

Hunt, R., Neal, A.M., Laffarga, J., Montserrat-Marti, G., Stockey, A., & Whitehouse, J. (1993) Mean relative growth rate. In G.A.F. Hendry & J.P. Grime (Eds.), Methods in comparative plant ecology. London: Chapman &Hall. pp. 98-102

Johnson I.R., and Thornley J.H.M., 1985. Dynamic model of the response of a vegetative grass crop to light, temperature and nitrogen. Plant, Cell and Environment, 8(7), 485-499.

Johnson, I.R. 1985. A meodel of the partitioning of growth between the shoots and roots of vegetative plants. Annals of Botany 55, 421-431.

Johnson, I.R. and Thornley, J.H.M.,1983. Vegetative crop growth model incorporating leaf area expansion and senescence, and applied to grass. Plant, Cell and Environment 6, 721-729.

Johnson, I.R. and Thornley, J.H.M., 1984. A model of instantaneous and daily canopy photosynthesis. Journal of theorical Biology,7, 531-545.

Johnson, I.R. and Thornley, J.H.M., 1987. A model of shoot:root partitioning with optimal growth. Annals of Botany 60, 133-142.

Johnson, I.R., Parsons, A.J. and Ludlow, M.M., 1989. Modelling photosynthesis in monocultures and mixtures. Aust. J. Plant Physiol. 16, 501-516.

Johnson, I.R., Riha, S.J. and Wilks, D.S., 1995 Modelling daily net canopy photosynthesis and its adaptation to irradiance and atmospheric CO2 concentration. Agricultural Systems 50, 1-35.

López-González, F.; Estrada-Flores, J. G.; Avilés-Nova, F.; Yong-Ángel, G.; Hernández -

Morales, P.; Martínez-Loperena, R.; Pedraza-Beltrán, P. E.; Castelán-Ortega, O. A., 2010. Agronomic evaluation and chemical composition of african star grass (Cynodon plectostachyus) in the southern región of the state of mexico. Tropical and Subtropical Agroecosystems, Vol. 12, 151-159

Ludlow, M.M. , 1985. Photosynthesis and dry matter production in C3 and C4 pasture plants, with special emphasis on tropical C3 legumes and C4 grasses. Australian journal of plant physiology, 12, 557-572.

Manson, W.G. and Burton, G., 1982. Harvest frequency and fertilizer effects on yields, quality and persistence of eight bermudagraseee. Agron. J. 74: 371-374.

Mislevy, P., F.G. Martin, B.J. Downs, and K.L. Singer., 1989. Response of stargrass to grazing management. Proc. Int. Grassl. Cong., 16th. p. 1017-1018. In R. Desroches (ed.) Proc. Int. Grassl. Congress, 16th, Nice, France. 4-11 Oct. 1989. The French Grassland Society, Versailles Cedex, France.

Mislevy, P. and William F. Brown, F.W., 1991. Management and utilization of complementary forages stargrass. Shortcourse . Agricultural Research and Education Center. University of Florida, Ona

Monteith J.L. 1981 Does light limit crop production? In: Johnson C.B. (Ed.) Physiological processes limiting plant productivity,. Butterworths, pp. 23-28

Mooney, H.A. and Ehleringer, J.R., Moore, A.D., Donnelly J.R. and Freer M., 1997. GRAZPLAN:Decision Support System for Australian Grazing Enterprises. III. Pasture Growth and Soil Moisture Submodels, and the GrassGro DSS. Agricultural Systems, 55 (4), 535-582.

Murtagh G.J. 1990 Variation in the supracritical nitrogen concentration of kikuyu grass. Communication in Soil Science and Plant Analyses 21, 207-220.

Ngijyen, P. M.T.; Araki, T and Kubota, F. J., 2005. Comparison of Growih Feature and Drought Tolerance between two High Productive Species, Kenaf (Hibicus cannabinus,C3-plant) and Napiergrass (*Pennisetum purpureum*, C4-plant. Fac. Agr., Kyushu Univ., 50 (2), 521-532

Ortega, L. and González, B., 1990. Efecto de la fertilización nitrogenada y frecuencia de corte sobre los rendimientos de materia seca y valor nutritivo del pasto estrella (*Cynodon nlemfuensis*). Revista de Agronomía (LUZ):7: 217 – 228

Parton, W.J. , 1984. Predicting soil temperatures in a shortgrass steppe. Soil Science 138 (2), 93-101.

Penman, H.L., 1956. Evaporation: an introductory survey, Netherlands J. of Agricultural Science 4, 9-29.

Porto, Petrônio Pinheiro, Fermino D., dos Santos G. T., Ferraz Lopes F. C., Cecato, U., Cóser A. C. Produção e composição química do leite, consumo e digestibilidade de forragens tropicais manejadas em sistema de lotação. R. Bras. Zootec. [online]. 2009, vol.38, n.8, pp. 1422-1431.

Pozo, P. P. del., Herrera, S. R., Chávez, D., Fernández L., García, M. 2000. Selección de variables morfoagronómicas que caracterizan el comportamiento del crecimiento del pasto estrella en condiciones de pastoreo. Cultivos Tropicales, 21: 37-40.

Richards, J.H., 1993. Physiology of pl.ants recovering from defoliation. In M.J. Baker (Ed.), Grasslands for our world Wellington: SIR Publising, pp. 46-54

Rimmington G.M., 1984. A model of the effect of interspecies competition for light on dry-matter production. Aust. J. Plant Physiol. 11, 227-286.

Rowell, D.L., 1994. Soil Science:Methods and Applications. Essex: Longman.

Silveira, V.C.P., 1999. Farmer Integrated Decision Model: integration between beef cattle and rice production in Rio Grande do Sul, Brazil. Ph D Thesis. University of Edinburgh.

Stanford, G., Frere, M.H. and Schwaninger, D.H., 1973. Temperature coefficient of soil nitrogen mineralization. Soil Science 115, 321-323.

Taiz, L. and Zeiger, E., 1991 Plant physiology, Redwood City, CA: Benjamin/Cummings.

Tilman, D., 1997. Mechanisms of plant competition. In: Crawley, M.J. (Ed.) *Plant Ecology*, Oxford: Blackwell Science. pp. 239-261.

Thornley J.H.M. and Verberne E.L.J., 1989. A model of nitrogen flows in grassland. Plant, Cell and Environment 12, 863-886.

Thornley J.H.M. and Johnson I.A., 1990. Plant and crop modelling. A mathematical approach to plant and crop physiology. Oxford University Press, 699pp.

Verberne E., 1992. Simulation of the nitrogen and water balance in a system of grassland and soil. DLO-Instituut voor Bodemvruchtbaarheid, Nota 258, 56 pp.

White, R.E., 198. Introduction to the principles and practice of soil science. Oxford: Blackwell Science.

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APPENDIX

Parameter used in the Star grass model.

Parameters	Description	Unit	Value	Origin
Alpha	Leaf photosynthetic efficiency	g CO_2 J^{-1}	10^{-5}	Johnson & Thornley, 1985
AlphaM$_s$	Respiration costs of mineral uptake	g C (g mineral) $^{-1}$	0.5	Johnson & Thornley, 1985
Ceiling	Ceiling parameter		2	
DecayR	Decay rate from dead root to litter	-	0.12	-
DecaySh	Decay rate from dead shoot to litter	-	0.1	-
DTC	Drought tolerance coefficient	-	0.5	-
Etam	Incremental specific leaf area parameter (maximum value ɳ)	m^2 (g structural dry matter)$^{-1}$	0.025	Johnson & Thornley, 1985
FC	Fractional carbon content of live plant structure	g C (g structure)$^{-1}$	0.45	Johnson & Thornley, 1985
FCR	Fractional carbon content of degradable structure	g C (g structure)$^{-1}$	0.4	Johnson & Thornley, 1985
FLamveg	Fraction of new shoot growth partitioned to lamina in vegetative stage	-	0.55	-
FLigSen	Fraction lignin in senescence stage	-	0.29	-
FLigVeg	Fraction lignin in vegetative stage	-	0.03	-
FN	Fractional nitrogen content of live plant structure	g N (g structure)$^{-1}$	0.015	-
FNR	Fractional nitrogen content of degradable structure	g N (g structure)$^{-1}$	0.072	-
FP$_s$	Fractional phosphorus content of live plant structure	g P (g structure)$^{-1}$	0.002	-
FPR	Fractional phosphorus content of degradable structure	g P (g structure)$^{-1}$	0.01	-

Parameters	**Description**	**Unit**	**Value**	**Origin**
Frostresist	Plant frost resistence	^{o} C	8.0	-
GammarOpt	Rate parameter for root turnover at optimum temperature	day^{-1}	0.035	Johnson & Thornley, 1985
GammashOpt	Rate of leaf appearance at optimum temperature	day^{-1}	0.15	Johnson & Thornley, 1985
K	Canopy extinction coefficient	-	0.60	Ludlow, 1985
LePhoto	Light saturated leaf gross photosynthetic rate parameter	(g CO2 /m2 (leaf)/sec.).	0.0014	Johnson & Thornley, 1985
MaxT	Maximum temperature for plant activity	^{o} C	45.0	Hanson et al., 1988
MC	Molecular mass of substrate carbon (sucrose) relative to ^{12}C	-	28.5	Johnson & Thornley, 1985
MinT	Minimum temperature for plant activity	^{o} C	11.0	Hanson et al., 1988
MN	Molecular mass of substrate nitrogen (nitrate) relative to ^{14}N	-	62	Johnson & Thornley, 1985
MNSoil	Minimum N soil without affect mobility	g m^2	2.0	-
MP	Molecular mass of substrate phosphorus (phosphate) relative to ^{15}P	-	95	-
MPSoil	Minimum P soil without affect mobility	g m^2	0.6	-
MrOptf	Maintenance coefficient of first root structural component	day	0.02	Johnson & Thornley, 1985
MrOpts	Maintenance coefficient of second root structural component	day	0.01	Johnson & Thornley, 1985
MrOptt	Maintenance coefficient of thirst root structural component	day	0.015	Johnson & Thornley, 1985
MrOptfo	Maintenance coefficient of fourth root structural component	day	0.01	Johnson & Thornley, 1985
MshOptf	Maintenance coefficient of first shoot structural component	day	0.01	Johnson & Thornley, 1985
MshOpts	Maintenance coefficient of second shoot structural component	day	0.02	Johnson & Thornley, 1985
MshOptt	Maintenance coefficient of thirst shoot structural component	day	0.015	Johnson & Thornley, 1985
MshOptfo	Maintenance coefficient of fourth shoot structural component	day	0.01	Johnson & Thornley, 1985
OptT	Optimum temperature for plant activity	^{o} C	30.0	Johnson & Thornley, 1985
Pi			3.1415927	
PMfrost	Proportion of mortality by frost		0.1	
SdN	Structural N degradation parameter	-	0.002	Johnson & Thornley, 1985

Parameters	Description	Unit	Value	Origin
SdP	Structural P degradation parameter	-	0.0002	-
SGR	Maximum growth rate	-	0.05	-
SRact	Structural root activity	-	0.5	-
Tau	Leaf transmission coefficient	-	0.1	Johnson & Thornley, 1985
Theta	Leaf photosynthesis parameter	-	0.87	Johnson & Thornley, 1985
Y	Yield factor for structural growth	-	0.75	Johnson & Thornley, 1985
Zetaslm	Incremental specific leaf area parameter	-	2.5	Johnson & Thornley, 1985

Variables used in the plant sub-model.

State variables	Description	Unit
Leaffo	Senescing leaves	g m^{-2}
Leaff	Growing leaves	g m^{-2}
Leafs	First fully expanded leaves	g m^{-2}
Leaft	Second fully expanded leaves	g m^{-2}
Racfo	Fourth live active root compartment	g m^{-2}
Racf	First live active root compartment	g m^{-2}
Racs	Second live active root compartment	g m^{-2}
Ract	Third live active root compartment	g m^{-2}
RDead	Root dead compartment	g m^{-2}
Rstfo	Fourth live structural root compartment	g m^{-2}
Rstf	First live structural root compartment	g m^{-2}
Rsts	Second live structural root compartment	g m^{-2}
Rstt	Third live structural root compartment	g m^{-2}
SC	Substrate carbon	g m^{-2}
ShDead	Shoot stand dead compartment	g m^{-2}
SN	Substrate nitrogen	g m^{-2}
SP	Substrate phosphorus	g m^{-2}
Stemfo	Senescing sheath-stem	g m^{-2}
Stemf	Growing sheath-stem	g m^{-2}
Stems	First fully expanded sheath-stem	g m^{-2}
Stemt	Second fully expanded sheath-stem	g m^{-2}

Rate variables

Variable	**Description**	**Unit**
ϕN	Recyclable fraction of N	g m^{-2}
ϕP	Recyclable fraction of P	g m^{-2}
γR	Dimensional function that determine the relative partitioning to root	-
γSh	Dimensional function that determine the relative partitioning to shoot	-
BTL	Biomass trampled by livestock	g m^{-2}
Cbalance	C balance in the plant	-
CGMax	C needed to maximum growth	g m^{-2}
CInput	Daily input of C from photosynthesis	g m^{-2}
ENplant	Effect of N in the plant (scalar)	-
ENSoil	Effect of N in the soil (scalar)	-
EShHarv	Effective shoot harvest	g m^{-2}
EShHarv	Effective harvest by plant or functional group	g m^{-2}
ESMPP	Effect of soil moisture on plant processes (scalar)	-
ETPP	Effect of temperature on plant processes (scalar)	-
FCDR	Flows of C from live root to dead root	g m^{-2}
FCDSH	Flows of C from live shoot to dead shoot	g m^{-2}
FCShD	Fractions of C in dead shoot material	g m^{-2}
Flam	Fraction of new shoot growth partitioned to lamina.	-
FNDR	Flows of N from live root to dead root	g m^{-2}
FNDSH	Flows of N from live shoot to dead shoot	g m^{-2}
FNShD	Fractions of N in dead shoot material	g N (g structure)$^{-1}$
FOLeaffo	Fluxes out of the fourth leaf compartment	g m^{-2}
FORAcfo	Fluxes out of the fourth active root compartment	g m^{-2}
FORfo	Total flux out of the live root compartment	g m^{-2}
FORStfo	Fluxes out of the fourth structural root compartments	g m^{-2}
FOShfo	Total flux out of the live shoot compartment	g m^{-2}
FOStemfo	Fluxes out of the fourth sheath-stem compartments	g m^{-2}
FPDR	Flows of P from live root to dead root	g m^{-2}
FPDSH	Flows of P from live shoot to dead shoot	g m^{-2}
FPShD	Fractions of P in dead shoot material	g P (g structure)$^{-1}$
Gc	Growth coefficient	g m^{-2}
GR	Synthesis of growth root structural dry matter	g m^{-2}
GSh	Synthesis of growth shoot structural dry matter	g m^{-2}
HarvSh	Harvest shoot dry weight	g m^{-2}
LAI	Leaf area index	-

Variable	**Description**	**Unit**
LeafReFo	Proportion of material in the fourth leaf compartment that remain on the field	g (g structure)$^{-1}$
LeafReT	Proportion of material in the third leaf compartment that remain on the field	g (g structure)$^{-1}$
Meff	Mycorrhizal effect (scalar)	-
NGMax	N needed to maximum growth	g m^{-2}
NP	Effective amount of N uptake by the plant	g m^{-2}
PGMax	P needed to maximum growth	g m^{-2}
PGR	Potential growth rate	g m^{-2}
Plig	Percentage of lignin ($Plig_s$)	g (g structure)$^{-1}$
PNUGR	Potential N uptake per gram of roots	g m^{-2}
PNU	Potential N uptake by roots	g m^{-2}
RDC	C dead root compartment	g m^{-2}
RDN	N dead root compartment	g m^{-2}
RDP	P dead root compartment	g m^{-2}
Rg	C loss by substrate pool to growth	g m^{-2}
Rm	C loss by substrate pool to maintenance	g m^{-2}
Rmug	C loss by substrate pool to mineral uptake	g m^{-2}
R	Live structural root	g m^{-2}
SCSR	C supplied from recycled roots	g m^{-2}
SCS	Supply of C from plant recycling	g m^{-2}
SCS	Rates of supply C from senescence	g m^{-2}
SCSSh	C supplied from recycled shoots	g m^{-2}
ShDC	C dead shoot compartment	g m^{-2}
ShDN	N dead shoot compartment	g m^{-2}
ShDP	P dead shoot compartment	g m^{-2}
ShHarvTot	Total sward harvest	g m^{-2}
Sh	Live structural shoot	g m^{-2}
SNSR	N supplied from recycled roots	g m^{-2}
SNS	Supply of N from plant recycling	g m^{-2}
SNS	Rates of supply N from senescence	g m^{-2}
SNSSh	N supplied from recycled shoots	g m^{-2}
SPSR	P supplied from recycled roots	g m^{-2}
SPS	Rates of supply P from senescence	g m^{-2}
SPSSh	P supplied from recycled shoots	g m^{-2}
StemReFo	Proportion of material in the fourth stem compartment that remain on the field	g (g structure)$^{-1}$
$StemReT_s$	Proportion of material in the third stem compartment that remain on the field	g (g structure)$^{-1}$

Variable	Description	Unit
$TEFL_s$	Time to end the first leaf as growing leaf	$days^{-1}$
$TEFoL_s$	Time to end the senescing leaf	$days^{-1}$
$TEFoR_s$	Time to end the fourth compartment root	$days^{-1}$
$TEFR_s$	Time to end the first compartment root	$days^{-1}$
$TESL_s$	Time to end as first fully expanded leaf	$days^{-1}$
$TESR_s$	Time to end the second compartment root	$days^{-1}$
$TETL_s$	Time to end the second fully expanded leaf	$days^{-1}$
$TETR_s$	Time to end the third compartment root	$days^{-1}$

Parameters used in the soil sub-model.

Parameters	Description	Unit	Value	Origin
Mineral sub-model				
CN	C:N ratio soil type dependence	-	10	-
CP	C:P ratio soil type dependence	-	110	-
DBD	Dry bulk density	g cm^3	1.17	ICAR Lab 2009
ESNo	Estimates of soil N mineralization potential	ppm	32.1	Parentoni et al., 1988
Kas	Maximum decomposition to secondary P	-	0.0016	Parton et al., 1987
Kfbd	Maximum faeces breakdown	-	0.024	-
Kfn	Maximum rate of N metabolic faeces decomposition	-	0.024	-
Krl	Maximum rate of metabolic root litter decomposition	-	0.05	-
Ksa	Maximum decomposition to available P	-	7.2^{-5}	Parton et al., 1987
Ksl	Maximum rate of metabolic surface litter decomposition	-	0.04	-
Kso	Maximum decomposition from secondary P to occluded P	-	3.3^{-8}	Parton et al., 1987
MinRate	Mineralization rate constant at 35 °C	-	0.09	Parentoni et al., 1988
NP	N:P ratio soil type dependence	-	11	-
RAE	Relative agronomic effectiveness	-	0.8	Leon et al., 1986
Water sub-model				
Aa	aa is a constant adjusted so $\sum Wf_z=1$	-	1.3185	-
Alpha	albedo reflection coefficient surface	-	0.2	Supit et al., 1994

Variables used in the soil sub-model.

State variables	Description	Unit
Mineral sub-model		
$CMet_{sl}$	C metabolic from surface litter	g m^{-2}
$CMet_{rl}$	C metabolic from root litter	g m^{-2}
NApl	N available to plant	g m^{-2}
NMfaeces	N metabolic from faeces	g m^{-2}
NMetsl	N metabolic from surface litter	g m^{-2}
NMetrl	N metabolic from root litter	g m^{-2}
PApl	P available to plant	g m^{-2}
PIfaeces	P inorganic from faeces	g m^{-2}
PMetsl	P metabolic from surface litter	g m^{-2}
PMetrl	P metabolic from root litter	g m^{-2}
SecP	Secondary P	g m^{-2}
Water sub-model		
W_1	actual soil moisture content in surface layer	cm^3H_2O cm^{-2}soil
W_z	actual soil moisture content in layer z (2 ... n)	cm^3H_2O cm^{-2}soil

Rate variables

Mineral sub-model	**Description**	**Unit**
CFsl	C flow from metabolic surface litter to soil organic matter	-
CFrl	C flow from metabolic root litter to soil organic matter	-
CNsl	Content of N immobilized from structural surface litter	g m^{-2}
CNrl	Content of N immobilized from root surface litter	g m^{-2}
CPsl	Content of P immobilized from structural surface litter	g m^{-2}
CPrl	Content of P immobilized from root surface litter	g m^{-2}
Csl	C in surface litter	g m^{-2}
Crl	C in root litter	g m^{-2}
ETBDf	Effect of temperature in breakdown of faeces	-
EMD	Effect of moisture on decomposition	-
ETD	Effect of temperature on decomposition	-
EMDf	Effect of moisture in faeces degradation	-

Mineral sub-model	**Description**	**Unit**
ETDf	Effect of temperature in faeces degradation	-
ETMFavol	N losses through ammonium gas in fertiliser	-
ETMUavol	N losses through ammonium gas in urine	-
Fmrl	Metabolic fraction of root litter	-
Fmsl	Metabolic fraction of surface litter	-
ISP	Flow from SecP to PApl	-
NL	Leaching N from root zone	g m^{-2}
PL	Leaching P from root zone	g m^{-2}
Lrl	Lignin in root litter	g m^{-2}
Lsl	Lignin in surface litter	g m^{-2}
Nlvaf	N loss through ammonium volatilization	g m^{-2}
Msoil	Moisture in soil (scalar)	-
Nfaeces	N from faeces	g m^{-2}
NImrl	N immobilised from metabolic root litter	g m^{-2}
NImsl	N immobilised from metabolic surface litter	g m^{-2}
NFa	N mineralization from faeces	g m^{-2}
NFe	N mineralization from fertiliser	g m^{-2}
NSOM	N mineralization from SOM	g m^{-2}
NStrusl	N structural from surface litter	g m^{-2}
NStrurl	N structural from root litter	g m^{-2}
NMrl	N mineralization from metabolic root litter	g m^{-2}
NMsl	N mineralization from metabolic surface litter	g m^{-2}
NSsl	N Imobilization from structural surface litter	g m^{-2}
NSrl	N Imobilization from structural root litter	g m^{-2}
Nsl	N in surface litter	g m^{-2}
NR	N from rain	g m^{-2}
Nrl	N in root litter	g m^{-2}
NU	N mineralization from urine	g m^{-2}
Nurine	N from urine	g m^{-2}
OclP	Flow from SecP to Oclude P	-
OSP	Flow from PApl to SecP	-
PFe	P from fertiliser to PApl	g m^{-2}
Pfaeces	P from faeces	g m^{-2}
PiFaeces	Inorganic fraction of P in faeces	-
PImsl	P from metabolic surface litter	g m^{-2}

Mineral sub-model	**Description**	**Unit**
PImrl	P from metabolic root litter	g m^{-2}
PFa	P mineralization from faeces	g m^{-2}
PMrl	P from metabolic root litter	g m^{-2}
PMsl	P from metabolic surface litter	g m^{-2}
PminSOM	P mineralization from SOM	g m^{-2}
PR	P from rain	g m^{-2}
Prl	P in root litter	g m^{-2}
PSecfe	P from fertiliser to SecP	g m^{-2}
Psl	P in surface litter	g m^{-2}
PStrusl	P structural from surface litter	g m^{-2}
PStrurl	P structural from root litter	g m^{-2}
Tsoil	Soil mean temperature	^{o}C

Water sub-model	**Description**	**Unit**
a_1	dimensionless soil moisture number	-
Beva	reduction factor accounting for the influence of soil moisture content of the surface layer on evaporation	-
$Btra_z$	reduction factor to account the effect of soil moisture on transpiration in layer z	-
ETO	potential evapotranspiration	mm day^{-1}
EVA	total actual soil evaporation	cm^3H_2O cm^{-2}soil day^{-1}
EVA_z	actual soil evaporation in layer z	cm^3H_2O cm^{-2}soil day^{-1}
EVAmp	potential bare soil evaporation	cm^3H_2O cm^{-2}soil day^{-1}
EVAp	potential soil evaporation	cm^3H_2O cm^{-2}soil day^{-1}
INF_z	infiltration in layer z=1, n-1	cm^3H_2O cm^{-2}soil day^{-1}
	percolation in layer z=n	
IRR	irrigation	cm^3H_2O cm^{-2}soil day^{-1}
LAI	leaf area index	-
RUN	runoff	cm^3H_2O cm^{-2}soil day^{-1}
TRA_z	actual plant transpiration in layer z	cm^3H_2O cm^{-2}soil day^{-1}
TRAmp	potential transpiration for a closed canopy	cm^3H_2O cm^{-2}soil day^{-1}
TRAp	potential plant transpiration	cm^3H_2O cm^{-2}soil day^{-1}
$RDef_z$	weighing factor accounting for withdrawn of moisture due to transpiration in layer z	-