Modelling of daily fluxes of water and carbon from shortgrass steppes

Y. Nouvellon a,*, S. Rambal b, D. Lo Seen a, M.S. Moran c, J.P. Lhomme d, A. Bégué a, A.G. Chehbouni e, Y. Kerr f

a CIRAD, 34093, Montpellier cedex 5, France
b DREAM-CEFE, CNRS (UPR 9056) 34293, Montpellier cedex 5, France
c USDA-ARS, Phoenix, AZ, USA
d ORSTOM/CICTUS, Hermosillo, Mexico
e ORSTOM/IMADES, Hermosillo, Mexico
f CESBIO-CNES, Toulouse, France

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Abstract

A process-based model for semi-arid grassland ecosystems was developed. It is driven by standard daily meteorological data and simulates with a daily time step the seasonal course of root, aboveground green, and dead biomass. Water infiltration and redistribution in the soil, transpiration and evaporation are simulated in a coupled water budget submodel. The main plant processes are photosynthesis, allocation of assimilates between aboveground and belowground compartments, shoots and roots respiration and senescence, and litter fall. Structural parameters of the canopy such as fractional cover and LAI are also simulated. This model was validated in southwest Arizona on a semi-arid grassland site.

In spite of simplifications inherent to the process-based modelling approach, this model is useful for elucidating interactions between the shortgrass ecosystem and environmental variables, for interpreting H₂O exchange measurements, and for predicting the temporal variation of above- and belowground biomass and the ecosystem carbon budget. Published by Elsevier Science B.V.

Keywords: Simulation model; Water and carbon fluxes; Shortgrass ecosystem; Arid environment; SALSA program

1. Introduction

Arid and semi-arid rangelands constitute nearly one third of the earth’s land surface (Branson et al., 1972). The broad extent of arid and semi-arid regions and their sensitivity to climatic variations and land-use changes make it imperative to improve our understanding of the hydrologic, atmospheric and ecological interactions and sustainability of these systems. The Semi-Arid Land Surface Atmosphere (SALSA) program was conceived as a long-term, multidisciplinary, monitoring and modelling effort to understand the complex interactions between hydrometeorological, biological and ecological processes occurring in semi-arid areas (Goodrich, 1994). The Upper San Pedro River Basin (USPB) was selected as the focal area for SALSA experiments. It spans the Mexico–US border from Sonora to Arizona and includes such major vegetation types as desert shrubsteppe, riparian...
communities, grasslands, oak savannah and ponderosa pine woodlands. As part of the integrated SALSA objectives, research is focused on methods for estimating water, carbon and energy balance of semi-arid rangelands over large areas. One of the objectives is to develop coupled soil-vegetation-atmosphere (SVAT) and plant growth models that can assimilate remote sensing data (Goodrich et al., 1998) to scale up local results to the landscape or regional scale.

Such an approach requires that any plant growth model realistically describes temporal variability in the amount of live and dead aboveground biomass, Leaf Area Index (LAI), and percent cover. This information is necessary to account for the influence of the vegetation canopy on the boundary layer (Lo Seen et al., 1997) and to couple with a land surface reflectance model while performing the assimilation of remotely sensed data (Lo Seen et al., 1995; Mougin et al., 1995). In this paper, we present a process-based plant growth model for shortgrass ecosystems developed in this perspective. The model has the same structure as the model of Mougin et al. (1995) which had been developed and validated for annual grasslands of the Sahel. The main improvements needed were relative to the presence of a root compartment whose dynamics cannot be ignored for perennial grassland ecosystems. These included allocation and translocation processes between aboveground and belowground plant compartments. Also, a more physically-based description of the evapotranspiration process (based on Penman-Monteith (Monteith, 1965)) together with the aerodynamic and soil resistances have been included in the water budget submodel. The model retains the most important environmental variables affecting plant growth processes and operates with a daily time step using readily available daily meteorological data and a limited number of plant and soil parameters.

In the study region, plant growth and the determination of peak biomass depend not only on highly unpredictable amounts of rainfall (Mc Mahon and Wagner, 1985), but also on carbohydrates previously stored in the root system. This storage pool is also a determining element in the response to grazing by large herbivores, in the survival during severe droughts, and in the domination of plant communities by perennial grass species. A realistic representation of belowground processes is therefore needed to successfully simulate aboveground growth patterns. The model simulates the seasonal and inter-annual courses of aboveground live and standing dead biomass as well as leaf area of the dominant perennial grasses. The living root compartment permits inter-annual simulation of important processes such as translocation of carbohydrates from roots to shoots during the early regrowth period at the end of the dry season and storage of photoassimilates in the belowground compartment. Also, as water is known to be the most important limiting factor on plant growth in semi-arid environments, soil water availability is computed in a water balance submodel. As in other published models (e.g. Feddes et al., 1978; Rambal and Cornet, 1982; Chen and Coughenour, 1994), plant growth and water fluxes processes are coupled in a functional and dynamic way.

While existing models account for more environmental effects on plant growth (e.g. Sauer, 1978; Detling et al., 1979; Coughenour et al., 1984; White, 1984; Hanson et al., 1988; Bachelet, 1989), some are difficult to parameterise (as stated in Hanson et al., 1985) or have been designed for other objectives. The model presented here retains only the most relevant processes so as to obtain a simplified yet realistic simulation. However, apart from simulating the one dimensional transfer of water and carbon, the model has some characteristics which makes it a candidate for spatialization using remote sensing data. For example, it has kept to a minimum the number of spatially variable input parameters (meteorological driving variables and site specific parameters) and also simulates surface variables which can be used in reflectance or radiative transfer models.

Here, this paper only gives a description of the model together with its validation on a grassland site of the USPB during three consecutive growing seasons. How the model is used in a scheme for including remote sensing data is not described at this stage, as this is the subject of ongoing work.

2. Model description

2.1. General model structure

The course of biomass of three main compartments of the vegetation cover: green live shoots, dead shoots and living roots are simulated on a daily time step.
The main processes involved in the plant growth submodel are photosynthesis, allocation of photosynthates to shoots and roots, translocation of carbohydrates from roots to shoots during the early growing period at the beginning of the wet season, respiration, and senescence. Many physiological processes such as photosynthesis and senescence are dependent on water availability in the root zone, which is simulated in a water balance submodel.

2.2. Vegetation growth model

The time course of biomass in the compartments is described by three differential equations with respect to time (t):

\[
\frac{dB_{ag}}{dt} = a_g P_g + T_{ra} - R_{ad} - S_a \tag{1}
\]

\[
\frac{dB_t}{dt} = a_t P_g - T_{ra} - R_{rt} - S_t \tag{2}
\]

\[
\frac{dB_{ad}}{dt} = S_a - L \tag{3}
\]

where \(B_{ag}\), \(B_t\), and \(B_{ad}\) are living aboveground biomass, living root biomass and standing dead biomass, respectively; \(P_g\) is the daily gross photosynthesis; \(a_g\) and \(a_t\) are the photosynthetic allocation partition coefficients to shoot and root compartments \((a_g + a_t = 1)\); \(T_{ra}\) represents the translocation of carbohydrates from the roots to the living aboveground compartment; \(R_{ad}\) and \(R_{rt}\) are total daily amounts of respiration from aboveground and root compartments, \(S_a\) and \(S_t\) represent the losses of biomass of the living shoots and roots due to senescence; and \(L\) represents the litter fall. \(B_{ag}\), \(B_t\), and \(B_{ad}\), are expressed in g DM m\(^{-2}\).

2.2.1. Photosynthesis

The daily carbon increment for the whole system results from photosynthesis. The gross daily canopy photosynthesis can be expressed as

\[
P_g = S_e \varepsilon_c \varepsilon_b f_1 (\Psi_1) f_2 (T) \tag{4}
\]

where \(S\) is the daily incoming solar radiation; \(\varepsilon_c\) the climatic efficiency (Photosynthetically Active Radiation (PAR)/S); \(\varepsilon_1\) the efficiency of interception by green leaves (or \(f_{\text{PAR}} = \text{intercepted PAR/PAR}\)); and \(\varepsilon_p\) is the energy conversion efficiency (or \(g\) assimilated CH\(_2\)O per unit of intercepted PAR). Functions \(f_1\) and \(f_2\) account for the constraints imposed by water stress, leaf water potential, \(\Psi_1\), and temperature, \(T\) respectively.

Water stress reduces photosynthesis by limiting the CO\(_2\) diffusion from air to leaf tissues as a result of stomatal closure. It is expressed as a function of leaf water potential as in Rambal and Cornet (1982):

\[
f_1 (\Psi_1) = \frac{(1.64 r_{s,\text{min}} + r_m + 1.39 r_a)}{(1.64 r_{s,\text{c}} + r_m + 1.39 r_a)} \tag{5}
\]

where \(r_{s,\text{c}}\) and \(r_{s,\text{min}}\) are current and minimum canopy stomatal resistance to water vapour; and \(r_m\) and \(r_a\) are mesophyll resistance and canopy boundary layer resistance to water vapour. The constants 1.64 and 1.39 relate to the ratio of diffusivities of CO\(_2\) and water vapour in the air at 20°C, and the ratio of the rate of transfer of CO\(_2\) and water vapour in the canopy boundary layer, respectively. \(r_{s,\text{c}}\) is calculated as a function of \(\Psi_1\) (see below). For C\(_4\) grasses, \(r_m\) is approximately 80 sm\(^{-1}\) (Gifford and Musgrave, 1973; Jones, 1992), and \(r_{s,\text{min}} 100\) sm\(^{-1}\) (Rambal and Cornet, 1982).

To calculate \(f_2\), we assume a null daily photosynthesis for temperatures smaller than a minimum temperature, and a linear relationship between photosynthesis and daily mean air temperature for temperatures ranging between minimum and optimum temperature. \(f_2 (T)\) can be expressed by:

\[
f_2 (T) = \begin{cases} 
0 & \text{if } T_a \leq T_{\text{min}} \\
1 - (T_{\text{opt}} - T)/(T_{\text{opt}} - T_{\text{min}}) & \text{if } T_{\text{min}} < T_a < T_{\text{opt}} \\
1 & \text{if } T_a \geq T_{\text{opt}}
\end{cases} \tag{6}
\]

where \(T_{\text{min}}\) and \(T_{\text{opt}}\) are the minimum and optimum temperature for gross photosynthesis of C\(_4\) grasses, respectively 7°C (Sauer, 1978) and 38°C (Penning de Vries and Dijittéye, 1982).

The climatic efficiency \(\varepsilon_c\) is fixed to 0.47 (Szeicz, 1974), and the interception efficiency \(\varepsilon_1\) is calculated as a function of green LAI \((L_g)\) and total LAI \((L_t)\):

\[
\varepsilon_1 = \left[1 - e^{(-k_c L_t)}\right] \frac{L_g}{L_t} \tag{7}
\]

\[
L_g = S_g B_{ag} \tag{8}
\]
\[ L_d = S_d B_{ad} \quad (9) \]
\[ L_t = L_g + L_d \quad (10) \]

where \( L_d \) is the dead biomass LAI; \( S_g \) and \( S_d \) are the specific leaf areas of the aboveground green biomass and the standing dead biomass [0.0105 m\(^2\) g\(^{-1}\) and 0.0110 m\(^2\) g\(^{-1}\), respectively (Goff, 1985)]; \( k_1 \) has been measured in a similar semi-arid grassland to be 0.58 (Nouvellon, 1999).

The energy conversion efficiency \( \varepsilon_b \) is dependent on the physiological age and therefore varies during the growing season. The depressing effect of leaf aging on \( \varepsilon_b \) is taken into account:

\[ \varepsilon_b = \varepsilon_{b\,\text{max}} f_3(\text{age}) \quad (11) \]

where \( \varepsilon_{b\,\text{max}} \) is the maximum energy conversion efficiency for young mature tissues, and \( f_3 \) is an empirical function representing the effect of aging on \( \varepsilon_b \). The physiological leaf age and \( f_3 \) were calculated as in the BLUEGRAMA model (Detling et al., 1979). \( \varepsilon_{b\,\text{max}} \) is usually taken as 8 g DM MJ\(^{-1}\) (Charles-Edwards et al., 1986).

### 2.2.2. Allocation

The available carbon pool resulting from photosynthesis is allocated into above-and belowground parts according to the allocation coefficients, \( a_g \) and \( a_r \), respectively. The daily amount which should be translocated from shoot to root \( T_{ar} \) is calculated according to Hanson et al. (1988). Their model is based on the assumption that a balance must be maintained between shoots and roots such that the amount of aboveground phytomass that the present root biomass can support is not exceeded. The excess amount of biomass in the shoots is determined as:

\[ B_{ax} = r_x B_{ag} - B_r \quad (12) \]

where \( r_x \) is the root to shoot ratio below which translocation occurs, set to 10 for perennial warm season grass (Hanson et al., 1988). If \( B_{ax} < 0 \), biomass flows from the shoots to the roots. If not, there is no allocation. \( T_{ar} \) is calculated so that the root to shoot ratio is fixed to \( r_x \) on a daily basis:

\[ r_x = \frac{B_t + T_{ar}}{B_{ag} - T_{ar}} \quad (13) \]

which, when combined with Eq. (12), means that:

\[ T_{ar} = \frac{B_{ax}}{1 + r_x} \quad (14) \]

Allocation coefficients are calculated assuming that \( T_{ar} \) should not exceed the gross photosynthesis \( P_g \):

\[ a_t = \begin{cases} 
T_{ar}/P_g & \text{if } T_{ar} < P_g \\
1 & \text{if } T_{ar} \geq P_g 
\end{cases} \quad (15) \]

The allocation coefficient for aboveground parts is calculated as:

\[ a_a = 1 - a_t \quad (16) \]

When the calculated shoot senescence exceeds a critical rate of 0.012, \( a_t \) is given a value of 0.71. This value is based on results of Singh and Coleman (1975) who found that during the late growth stage of the semi-arid shortgrass blue grama (\textit{Bouteloua gracilis} (H.B.K.) Lag.), 71% of the photoassimilated radiocarbon moved to roots.

#### 2.2.3. Root to Shoot Translocation

Translocation of carbohydrates from roots to shoots, \( T_{ra} \), occurs during the early season regrowth or later in the season if some process such as grazing has removed a critical amount of green biomass. The model used to calculate \( T_{ra} \) is the one proposed by Hanson et al. (1988), which necessitates three conditions for this process to occur: (1) The average 10 day soil temperature must be greater than 12.5°C; (2) the average 5 day soil water potential must be greater than –1.2 MPa, and; (3) \( B_t > r_x B_{ag} \).

If all these conditions are met:

\[ T_{ra} = t_t B_t \quad (17) \]

where \( t_t \) is the proportion of root biomass translocated daily to shoots (=0.005 at 25°C). We assume that translocation is temperature dependent with a \( Q_{10} = 3 \).

#### 2.2.4. Respiration

Total respiration \( R_t \) is the sum of total aboveground respiration, \( R_{at} \), and total root respiration, \( R_{rt} \). For \( C_4 \) grasses photorespiration is negligible. Thus, the aboveground respiration \( R_{at} \) can be expressed as the sum of maintenance and growth respiration:

\[ R_{at} = m_a f_4(T) B_{ag} + g_a (a_a P_g + T_{ra}) \quad (18) \]
and the total root respiration $R_{rt}$ is expressed as:

$$R_{rt} = m_r f_4(T) B_t + g_r \left( a_t P_g \right)$$  \hspace{1cm} (19)$$

where $m_a$ and $m_r$ are the maintenance respiration coefficients for aboveground and root biomass; $f_4(T)$ represents the effect of temperature on maintenance respiration ($Q_{10} = 2$); $g_a$ and $g_r$ are the growth respiration coefficients for aboveground and root compartment, respectively. These coefficients represent the cost for producing new biomass (McCree, 1970; Amthor, 1984). $g_a$ and $g_r$ are approximately 0.25 (McCree, 1970; Penning de Vries and Djitèye, 1982; Amthor, 1984; Ruymy et al., 1996) and 0.2 (Bachelet, 1989), respectively. Shoot maintenance respiration is 0.02 g DM per g DM per day at 20°C (Amthor, 1984). Root maintenance respiration is 0.002 g C (g metabolic C day)$^{-1}$ (Bachelet, 1989) at 20°C. Assuming 60% of structural material in roots (Bachelet, 1989), this led to an overall maintenance respiration rate of 0.0008 g DM per g DM per day.

2.2.5. Senescence

The amounts of green aboveground biomass and root biomass which die each day, $S_a$ and $S_r$, are calculated as:

$$S_a = d_a B_{ag}$$ \hspace{1cm} (20)

$$S_r = d_r B_t$$ \hspace{1cm} (21)

where $d_a$ and $d_r$ are the death rate for aboveground part and roots, respectively. $d_a$ is calculated as a function of leaf physiological age, plant water potential and daily minimum temperature according to Detling et al. (1979). $d_a$ varies from 0.0074 for young well-watered shoots, up to 0.14 for old shoots at −5 MPa. These values are close to those used by Coughenour et al. (1984) and Bachelet (1989). $d_r$ is assumed to be constant during the year, and was calculated based on the results of Anway et al. (1972) who estimated the root biomass replacement rate of blue grama as 25% per year.

2.2.6. Litterfall

Transfer of material from standing dead biomass to litter can be caused by wind, rain and dust (Clark and Paul, 1970). We assumed that the effects of dust and wind were negligible compared to the effect of rain. The rate of standing dead biomass pushed down by rain on a given day ($k_r$) was calculated as in Hanson et al. (1988):

$$k_r = 0.25 \left[ 1 - \exp \left( -0.025 R \right) \right]$$  \hspace{1cm} (22)$$

where $R$ is the total daily precipitation (in mm), and −0.025 is the tolerance of standing dead biomass to precipitation for warm season grass (Hanson et al., 1988). Daily litter production ($L_a$) is thus:

$$L_a = k_r B_{ad}$$  \hspace{1cm} (23)$$

2.3. Water balance model

The water balance model follows the general scheme described in Leenhardt et al. (1995). It uses a simplified two layer canopy evapotranspiration model coupled with a multilayered soil water balance. A top 0–0.02 m soil layer controls the direct evaporation and two deeper layers (0.02–0.15 and 0.15–0.60 m) participate in both evaporation and plant water uptake.

2.3.1. Soil water balance

Each soil layer is characterised by its water content $\theta$ and water potential $\psi$; these two variables are related by the widely used power-function model for the retention curve first proposed by Brooks and Corey (1964) and further simplified by Campbell (1974) and Saxton et al. (1986):

$$\psi = A \theta^b$$  \hspace{1cm} (24)$$

Changes in soil water content are simulated by a multilayered bucket model with a daily time step. The water infiltrating the soil is distributed down the profile according to the bucket model: the soil layers are filled successively from top to bottom until $\theta$ reaches field capacity. We assumed that field capacity is equal to the water content at $-33$ kPa soil water potential. The daily change of the soil water content of the first layer of depth $z_1$ is:

$$\Delta \theta_1 = \frac{R - E_{s1} - D_1}{z_1}$$  \hspace{1cm} (25)$$

where $R$ is the amount of rainfall (mm), $D_1$ the drainage from the first layer to the second (mm); and $E_{s1}$ is the evaporation from the first layer (mm). In the two other layers, the daily changes are
\[ \Delta \theta_i = \frac{D_{i-1} - E_{si} - Q_{ci} - D_i}{z_i - z_{i-1}} \]  

(26)

where \( i \) is the soil layer number; \( D_{i-1} \) the water infiltrated from the previous layer (mm); and \( Q_{ci} \) is the water extracted from the layer \( i \) for transpiration (see next section) (mm). Drainage from a layer \( i \) to layer \( i+1 \) occurs when \( \theta_i > \theta_{fi} \), where \( \theta_{fi} \) is the field capacity (mm\(^3\) mm\(^{-3}\)).

### 2.3.2. Estimation of actual evapotranspiration

The total evaporation from the sparse discontinuous grass canopy is calculated as the sum of bare soil evaporation \( E_s \) and canopy evaporation \( E_C. E_C \) and \( E_s \) are calculated empirically from the evapotranspiration of a continuous canopy and evaporation of a bare soil regardless of their percentage covers. If \( f_{vg}, f_{vd} \) and \( f_i \) are respectively, the cover fraction of green vegetation, dead vegetation and bare soil (\( f_{vg} + f_{vd} + f_i = 1 \)), \( E_C \) and \( E_s \) are calculated based on Penman-Monteith equation (Monteith, 1965) as:

\[ E_c = f_{vg} \left[ \frac{sA + \rho c_p D/r_{ac}}{(s + \gamma(1 + r_{ac}/r_{as}))\lambda} \right] \]  

(27)

\[ E_s = f_{vd} \left[ \frac{sA + \rho c_p D/r_{as}}{(s + \gamma(1 + r_{ac}/r_{as}))\lambda} \right] \]  

(28)

where \( A \) is the available energy, which is the difference between net radiation \( R_n \) and soil heat flux \( G. R_n \) and \( G \) are estimated as follows:

\[ R_n = S_n + L_n \]  

(31)

where \( S_n \) is the net short-wave radiation; and \( L_n \) is the net long-wave radiation. \( S_n \) is given by:

\[ S_n = S(1 - \alpha) \]  

(32)

where \( S \) is the incoming short-wave radiation; and \( \alpha \) is the albedo of the surface (taken to be equal to 0.3 for a bare soil and 0.2 for dense canopy). \( L_n \) is calculated with a Brunt-type equation (Shuttleworth, 1993).

\[ L_n = -c(a_c + b_c \sqrt{e})\sigma(T_a + 273.2)^4 \]  

(33)

where \( c \) is an adjustment coefficient for cloud cover; \( e \) is the vapour pressure in KPa; \( a_c \) and \( b_c \) are regression coefficients (0.34 and 0.14, respectively); \( \sigma \) is the Stefan-Boltzmann constant; and \( T_a \) is the mean air temperature in °C. The coefficient of adjustment for cloud cover is given by:

\[ c = a_c \left( \frac{S}{S_o} \right) + b_c \]  

(34)

where \( S_o \) is the solar radiation for clear skies, calculated as a function of day of year and latitude following Perrin de Brichambaut and Vauge (1982); \( a_c = 1.35 \) and \( b_c = -0.35 \) for arid areas (Shuttleworth, 1993). For a bare soil from which water can evaporate during the whole day, \( L_n \) is calculated over 24 h and \( G \) is neglected because the diurnal gain is assumed to balance the nocturnal loss. For a full canopy, \( G \) is taken
equal to 5% of \((S_1 + L_1)\), and \(L_1\) is calculated over the daylength.

2.3.4. Resistance models

The bulk stomatal resistance of the canopy \(r_{sc}\) is calculated as a function of leaf water potential \(\Psi_i\) (MPa) as:

\[
r_{sc} = r_{s\text{min}} \left[ 1 + \left( \frac{\Psi_i}{\Psi_{1/2}} \right)^n \right] \tag{35}
\]

where \(r_{s\text{min}}\) is the minimal stomatal resistance observed in optimal conditions; \(\Psi_{1/2}\) the leaf water potential corresponding to a 50% stomatal closure (MPa); and \(n\) is an empirical parameter (Rambal and Cornet, 1982).

The soil surface resistance \(r_{ss}\) is calculated as a function of the water content of the first soil layer by means of an empirical relationship (Camillo and Gurney, 1986):

\[
r_{ss} = 4140 (\theta_{s1} - \theta_1) - 805, \quad \text{(s m}^{-1}) \tag{36}
\]

where \(\theta_1\) represents the water content of the top soil \(0–0.02\ m\) layer \((m^3\ H_2O\ m^{-3}\ \text{soil})\); \(\theta_{s1}\) is the soil water content at saturation \((m^3\ m^{-3})\) of the ground surface layer.

The aerodynamic resistances are calculated as:

\[
r_a = \frac{\ln^2[(z_t - d)/z_0]}{(k^2 U)} \tag{37}
\]

where \(z_t\) is the reference height where wind speed \(U\) and air humidity are measured; \(k\) the von Karman constant \((0.41)\); \(d\) the zero plane displacement; and \(z_0\) is the roughness length calculated as a fraction of the mean height \(h_c\) of the vegetation canopy, \(z_0 = 0.1 h_c\) and \(d = 0.67 h_c\). For a bare soil, \(z_t = 0.01\ m\) and \(d = 0. h_c\) is approximately \(0.12\ m\) for this shortgrass ecosystem (Goff, 1985; Weltz et al., 1994).

2.3.5. Calculation of leaf water potential

The leaf water potential \(\Psi_i\) is needed to calculate the canopy resistance and hence the canopy transpiration. It is obtained iteratively by equating \(E_c\) [given by Eq. (27) in which \(r_{sc}\) is replaced by its formulation in Eq. (35)] with the sum of the water amounts extracted by the roots from the different soil layers, as calculated following an analogy with Ohm’s law:

\[
Q_i = \frac{(\Psi_{si} - \Psi_i)}{r_{spi}} \tag{38}
\]

where \(r_{spi}\) and \(\Psi_{si}\) are the soil-plant resistance and the water potential in the \(i\)th soil layer. At the daily time scale used in the model, we assume that internally stored water does not contribute significantly to transpiration and that the canopy generates a water potential just sufficient to equal transpiration and root water uptake (Rambal and Cornet, 1982). At lower time scale, models have been proposed to account for the variation of water storage in the canopy (Kowalik and Turner, 1983). \(r_{spi}\) is a linear function of root biomass in the \(i\)th layer, and \(\Psi_{si}\) is inferred from \(\theta_i\) through the soil retention curve \(\Psi_{si} = f(\theta)\). \(\Psi_i\) of day \(n\) is calculated from \(\Psi_{si}\) of day \(n-1\), and is used to calculate \(r_{sc}\) and \(E_c\) of day \(n\).

3. Calibrating and testing the model

3.1. Site description and experimental setup

The model was validated against data obtained by the USDA-ARS Southwest Watershed Research Center at the Kendall site from June 28 1990 through the end of 1992. The site is located in the Walnut Gulch Experimental Watershed (31°43’N 110°W) within the San Pedro Basin in southeastern Arizona (Renard et al., 1993). The topography is characterised by gently rolling hills, with a mean elevation of 1526 m ASL. The annual precipitation ranges from 250 to 500 mm with approximately two thirds falling during the ‘monsoon season’ from July to September (Osborn et al., 1972). Summer precipitation is characterized by convective thunderstorms of limited extent resulting from moist unstable air masses coming from the Gulf of Mexico, whereas winter precipitation results from frontal storms characterised by long duration, low intensity and large area coverage (Sellers and Hill, 1974). Over a year, daily global radiation and PAR are 19.1 and 9.0 MJ, respectively. Maximum global radiation occurs in June (26.8 MJ per day), and the minimum in December (10.0 MJ per day). The mean annual temperature is 16.7°C and the mean monthly temperature ranges from 8 to 27°C. Extreme temperatures of −8.6 and 40.5°C have been recorded in December/January and June/July, respectively.
average frost-free season is 239 days. Relative humidity is low throughout the year (average value = 39.5%). April–June have the lowest relative humidity and August and September the highest. During December and January, high values are also common due to effects of frontal rain events. The mean annual wind speed is about 3.6 m s\(^{-1}\).

The vegetation cover within the Kendall study area is dominated by C\(_4\) perennial grasses whose dominant species are black grama (Bouteloua eriopoda (Torr.) Torr.), curly mesquite (Hilaria belangeri (Steud.) Nash), hairy grama (Bouteloua hirsuta (Lag.) and three-awn (Aristida hamulosa (Henr.)) (Weltz et al., 1994), and whose root systems are almost exclusively restricted to the upper 60 cm of soil (Cox et al., 1986; Nouvellon, 1999).

Rainfall was monitored at the Kendall site, using automated weighing raingauges (Renard et al., 1993). Other ancillary meteorological data included wind speed, measured at 2 m Above Ground Level (AGL) using a R. M. Young photo-chopper cup anemometer, solar radiation, measured at 3.5 m AGL using a LiCor silicon pyranometer model LI-200SZ, and relative air humidity and air temperature, measured at 2 m AGL using a Campbell Scientific Inc. (CSI) temperature and relative humidity sensor model 207 contained in a Gill radiation shield (Kustas and Goodrich, 1994; Kustas et al., 1994). Net radiation was also measured, at 3.3 m AGL with a REBS Q*6 net radiometer (Kustas et al., 1994; Stannard et al., 1994), as well as soil moisture from Time Domain Reflectimetry (TDR) probes spaced every 0.1 m down to a depth of 0.6 m (Amer et al., 1994).

Biomass and LAI were estimated at the Kendall site at 2 weeks to 1 month intervals during the growing seasons, and approximately at 1.5 month intervals between the growth periods (Tiscareno-Lopez, 1994). Each estimation of live and dead standing biomass resulted from clipping plants within eight 0.5 m \(\times\) 1.0 m quadrats, and weighing them after a 24h drying period at 70°C.

3.2. Model parameters

A number of attempts have been made to predict retention curves from soil texture data (e.g. Arya and Paris, 1981; Rawls et al., 1982; De Jong, 1983 and Saxton et al., 1986). These attempts have not been completely successful (e.g. Ahuja et al., 1985). Nevertheless, the relationship between soil water content and soil water potential is strongly dependent on soil texture. In this study, we assume the broad-based regression equations proposed by Saxton et al. (1986) which adequately predict the two parameters of the moisture retention curves (Eq. (24)) as a function of measured soil particle size distribution in each soil layer. For the 0.02–0.15 and 0.15–0.60 m soil layers the \(b\) parameters calculated following this regression and measured soil textures are \(-8.71\) and \(-8.51\), respectively. These values are rather low compared to that obtained by Clapp and Hornberger (1978) from the statistics of moisture parameters for sandy clay loam soils \((-7.12 \pm 2.43\).

Parameters describing root biomass distribution were set following the results of Cox et al. (1986) who measured root biomass distribution on a similar semi-arid grassland close to this site in August 1983. According to their results, 73% of root biomass was found in the first 0.15 m. These results were close to those of Singh and Coleman (1975) who found on a shortgrass prairie, dominated by blue grama, that 68–78% of the total root biomass occurred between 0 and 0.20 m. Other model parameter values are summarised in Table 1.

Initial water content in the soil layers, as well as dead and living aboveground biomass were measured. Initial root biomass was fitted so that simulated aboveground biomass compared well with the first measurements of the 1990 growing season. As expected, this value (444 g DM m\(^{-2}\)) was close to but less than the value obtained at a later stage during the 1983 growing season (Cox et al., 1986).

3.3. Simulation results

Simulation started before the 1990 monsoon season on June 28 [Day Of Year (DOY) 179] and ran continuously throughout end of 1992. Daily values of rainfall and vapour pressure deficit (VPD) are shown on Fig. 1. Annual rainfall amounts were 412, 369 and 434 mm for years 1990, 1991 and 1992, respectively (in 1990, 349 mm fell between DOY 179 and 365; see Table 2). The rainfall patterns are of prime importance for perennial grass growth and survival. By compar-
Table 1
List of parameters used in the model

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Symbol</th>
<th>Equation</th>
<th>Value</th>
<th>Unit</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Climatic efficiency</td>
<td>$c$</td>
<td>Eq. (4)</td>
<td>0.47</td>
<td></td>
<td>Szeicz, 1974</td>
</tr>
<tr>
<td>Minimum canopy stomatal resistance</td>
<td>$r_{smin}$</td>
<td>Eq. (5)</td>
<td>100</td>
<td>s m$^{-1}$</td>
<td>Rambal and Cornet, 1982</td>
</tr>
<tr>
<td>Mesophyll resistance</td>
<td>$r_m$</td>
<td>Eq. (5)</td>
<td>80</td>
<td>s m$^{-1}$</td>
<td>Gifford and Musgrave, 1973; Jones, 1992</td>
</tr>
<tr>
<td>Minimum temperature for gross photosynthesis</td>
<td>$T_{min}$</td>
<td>Eq. (6)</td>
<td>7.0</td>
<td>$^\circ$C</td>
<td>Sauer, 1978</td>
</tr>
<tr>
<td>Optimum temperature for gross photosynthesis</td>
<td>$T_{opt}$</td>
<td>Eq. (6)</td>
<td>38.0</td>
<td>$^\circ$C</td>
<td>Penning de Vries and Dijèye, 1982</td>
</tr>
<tr>
<td>Extinction coefficient of radiation in the canopy</td>
<td>$k_1$</td>
<td>Eq. (7)</td>
<td>0.58</td>
<td></td>
<td>Nouvellon, 1999</td>
</tr>
<tr>
<td>Specific leaf areas of the aerial green biomass $S_g$</td>
<td>$S_g$</td>
<td>Eq. (8)</td>
<td>0.0105</td>
<td>m$^2$ g$^{-1}$</td>
<td>Goff, 1985 (measured on Kendall site)</td>
</tr>
<tr>
<td>Specific leaf areas of the aerial dead biomass $S_d$</td>
<td>$S_d$</td>
<td>Eq. (9)</td>
<td>0.0110</td>
<td>m$^2$ g$^{-1}$</td>
<td>Goff, 1985 (Measured on Kendall site)</td>
</tr>
<tr>
<td>Maximum energy conversion efficiency</td>
<td>$e_{bmax}$</td>
<td>Eq. (11)</td>
<td>8</td>
<td>g DM MJ$^{-1}$</td>
<td>Charles-Edwards et al., 1986</td>
</tr>
<tr>
<td>Minimum root to shoot ratio</td>
<td>$r_x$</td>
<td>Eq. (12)</td>
<td>10.0</td>
<td></td>
<td>Hanson et al., 1988</td>
</tr>
<tr>
<td>Proportion of root biomass daily translocated to shoots</td>
<td>$t_r$</td>
<td>Eq. (17)</td>
<td>0.005</td>
<td></td>
<td>Hanson et al., 1988</td>
</tr>
<tr>
<td>Maintenance respiration coefficient for aerial biomass</td>
<td>$m_a$</td>
<td>Eq. (18)</td>
<td>0.02 (at 20$^\circ$C)</td>
<td>g DM per g DM per day</td>
<td>Amthor, 1984</td>
</tr>
<tr>
<td>Maintenance respiration coefficient for root biomass</td>
<td>$m_r$</td>
<td>Eq. (18)</td>
<td>0.0008 (at 20$^\circ$C)</td>
<td>g DM per g DM per day</td>
<td>see text</td>
</tr>
<tr>
<td>Growth respiration coefficient for aerial biomass</td>
<td>$g_a$</td>
<td>Eq. (18)</td>
<td>0.25</td>
<td></td>
<td>McCree, 1970</td>
</tr>
<tr>
<td>Growth respiration coefficient for root biomass</td>
<td>$g_r$</td>
<td>Eq. (18)</td>
<td>0.2</td>
<td></td>
<td>Bachelet, 1989</td>
</tr>
<tr>
<td>Death rate for aerial compartment</td>
<td>$d_a$</td>
<td>Eq. (20)</td>
<td>0.0074 to 0.14</td>
<td>g DM per g DM per day</td>
<td>Detling et al., 1979</td>
</tr>
<tr>
<td>Death rate for root compartment</td>
<td>$d_r$</td>
<td>Eq. (21)</td>
<td>0.00078</td>
<td>g DM per g DM per day</td>
<td>see text and Nouvellon, 1999</td>
</tr>
<tr>
<td>Extinction coefficient of radiation coming from zenith in the canopy</td>
<td>$k_2$</td>
<td>Eqs. (29) and (30)</td>
<td>0.36</td>
<td></td>
<td>Nouvellon, 1999</td>
</tr>
<tr>
<td>Albedo</td>
<td>$\alpha$</td>
<td>Eq. (32)</td>
<td>0.3 (soil) 0.2 (canopy)</td>
<td>MPa</td>
<td>Rambal and Cornet, 1982</td>
</tr>
<tr>
<td>Leaf water potential corresponding to a 50% stomatal closure</td>
<td>$\Psi_{1/2}$</td>
<td>Eq. (35)</td>
<td>0.6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shape parameter</td>
<td>$n$</td>
<td>Eq. (35)</td>
<td>5</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

ing the monsoon precipitation of 1990 and 1991, it can be noted that the 1990 precipitation pattern was more favourable to plant growth due to both its higher amount and its distribution pattern. For year 1992, it should be noted that rainfall during the spring was higher than normal. The VPD was less during the 1990 monsoon season than during the two other monsoon seasons.

Net radiation of the grassland, calculated as the sum of simulated net radiation of bare soil, dead canopy and live canopy weighted by their fractional covers had an annual mean value of 9.1 and 9.2 MJ per day for
year 1991 and 1992, that is 47% of the total incident radiation.

Simulated daily transpiration, soil evaporation and evapotranspiration are shown in Fig. 2. Daily ET was highly variable due to the variation of potential evapotranspiration (PET (Lhomme, 1997)) and soil water availability. Due to the low plant fractional cover, transpiration was generally less than soil evaporation. From June 28 1990 through the end of 1992, accumulated transpiration, evaporation and actual evapotranspiration were 212, 877 and 1089, respectively. Thus, the model predicted that evaporation represented 80% of the ET, while transpiration represents only 20% of total ET. Deep drainage below 0.60 m was predicted to be only 5% of total precipitation.

Simulated soil water content in layers 2–15 and 15–60 cm are shown in Fig. 3 for year 1990. Comparison with measurements showed that soil water content was well simulated and soil water regime generally followed the patterns described by Herbel and Gibbens (1987).

Simulated living aboveground biomass and living root biomass are shown in Fig. 4. Results show that living aboveground biomass simulations closely followed measurements with an overestimation during spring, 1992. This could have been caused by the inability of the model to account for small changes in the floristic composition of the vegetation canopy and particularly the presence of C₃ and C₄ annual grasses or forbs at the beginning of the wet season. Following the rainfall pattern, plant growth is bimodal. Generally, the model shows limited plant growth in the spring when temperatures and soil water conditions are favourable. However, exceptionally favourable spring rains (as in 1992) can produce a very high modelled plant growth. In May and June, most of the aboveground vegetation dries up due to soil limitations. The most significant growth then occurs during the summer.
Table 2
Terms of the water, energy and carbon budgets for three consecutive years (g C m\(^{-2}\) are obtained from g DM m\(^{-2}\) by dividing by 2.5, considering biomass is mainly composed of \((\text{CH}_2\text{O})_n\))

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Rainfall</td>
<td>mm</td>
<td>349</td>
<td>369</td>
<td>434</td>
</tr>
<tr>
<td>Global radiation</td>
<td>MJ</td>
<td>3679</td>
<td>7036</td>
<td>6916</td>
</tr>
<tr>
<td>Net radiation</td>
<td>MJ</td>
<td>1688</td>
<td>3330</td>
<td>3346</td>
</tr>
<tr>
<td>Total latent flux</td>
<td>MJ</td>
<td>709</td>
<td>837</td>
<td>1126</td>
</tr>
<tr>
<td>Evapotranspiration</td>
<td>mm</td>
<td>289</td>
<td>341</td>
<td>459</td>
</tr>
<tr>
<td>Evaporation from soil</td>
<td>mm</td>
<td>205</td>
<td>306</td>
<td>366</td>
</tr>
<tr>
<td>Transpiration</td>
<td>mm</td>
<td>84</td>
<td>35</td>
<td>93</td>
</tr>
<tr>
<td>Gross photosynthesis</td>
<td>g C m(^{-2})</td>
<td>390</td>
<td>124</td>
<td>341</td>
</tr>
<tr>
<td>Net photosynthesis</td>
<td>g C m(^{-2})</td>
<td>301</td>
<td>54</td>
<td>219</td>
</tr>
<tr>
<td>Total respiration</td>
<td>g C m(^{-2})</td>
<td>179</td>
<td>135</td>
<td>210</td>
</tr>
<tr>
<td>Aboveground respiration</td>
<td>g C m(^{-2})</td>
<td>90</td>
<td>70</td>
<td>122</td>
</tr>
<tr>
<td>Root respiration</td>
<td>g C m(^{-2})</td>
<td>90</td>
<td>65</td>
<td>88</td>
</tr>
<tr>
<td>Allocation to roots</td>
<td>g C m(^{-2})</td>
<td>264</td>
<td>40</td>
<td>185</td>
</tr>
<tr>
<td>TNPP</td>
<td>g C m(^{-2})</td>
<td>211</td>
<td>-11</td>
<td>130</td>
</tr>
<tr>
<td>ANPP</td>
<td>g C m(^{-2})</td>
<td>44</td>
<td>35</td>
<td>51</td>
</tr>
<tr>
<td>BNPP</td>
<td>g C m(^{-2})</td>
<td>168</td>
<td>-45</td>
<td>80</td>
</tr>
<tr>
<td>Total death</td>
<td>g C m(^{-2})</td>
<td>84</td>
<td>99</td>
<td>105</td>
</tr>
<tr>
<td>Shoot death</td>
<td>g C m(^{-2})</td>
<td>46</td>
<td>35</td>
<td>51</td>
</tr>
<tr>
<td>Root death</td>
<td>g C m(^{-2})</td>
<td>38</td>
<td>64</td>
<td>54</td>
</tr>
<tr>
<td>Root change</td>
<td>g C m(^{-2})</td>
<td>129</td>
<td>-109</td>
<td>26</td>
</tr>
</tbody>
</table>

\(^{a}\) From June 28.

season. For each year, peak biomass was obtained in mid-September (90 g DM m\(^{-2}\) in 1990; 65 g DM m\(^{-2}\) in 1991; and 72 g DM m\(^{-2}\) in 1992). The highest yield, obtained in summer 1990, was produced by a favourable pattern of rainfall.

Root biomass decreases between growing seasons due to respiration and senescence. This decrease is accelerated during the start of vegetation growth in Spring and Summer due to translocation of carbohydrates from roots to young shoots. After shoot development, when the amount of photoassimilated carbon allocated from the shoots to roots exceed root respiration and senescence, root biomass increases, and reaches its maximum value at the end of the growing season (end of September/beginning of October). Root biomass increase was very high during the monsoon season of 1990, but moderate in 1992 and negligible in 1991.

Maximum LAI for monsoon seasons 1990–1992 were 0.94, 0.68 and 0.74, respectively. Regression analysis showed that simulated and measured green LAI compared well with a coefficient of determination of 0.87 (Fig. 5).

Results for the carbon budget are shown in Table 2. Gross and net photosynthesis were highly variable from 1 year to the next. In 1990, gross photosynthesis was 3.1 times that of year 1991. The variability of simulated Aboveground Net Primary Productivity (ANPP) was much less than that of simulated gross and net photosynthesis, explained by the fact that the years with higher amounts of gross photosynthesis were also those with higher allocation of carbon to the roots. Simulated Belowground Net Primary Productivity (BNPP) for year 1991 was negative because simulated carbon allocation to the roots was lower than that consumed in respiration or translocated to the shoots. Root respiration is the sum of growth respiration and maintenance respiration and thus depends on the amount of carbon allocated to the roots and the root biomass. For years 1990 and 1992, higher allocation to the roots led to a higher root growth respiration and total root respiration.

4. Discussion

Net radiation represented 47% of total global radiation over the 3 years modelled in this study. This value is close to that found by Lapitan and Parton (1996) on a shortgrass steppe in North-Central Colorado.
evaporation processes used on average 32% of the net radiation. The amount of transpiration was found to be low when compared to evaporation. On an annual basis, modelled transpiration represented only 20% of actual evapotranspiration because of the low fractional cover of green vegetation even during the growing season. Furthermore, this region is often characterised by small inefficient rain events that wet only the surface soil layer.

Mean annual ANPP and TNPP (Aboveground and Total Net Primary Productivity) were 107 and 276 g DM m\(^{-2}\), respectively. Thus, the ratio of ANPP/TNPP was 0.39. For semi-arid grasslands, values for this ratio range between 0.25 and 0.6 (Sims and Singh, 1978; Milchunas and Lauenroth, 1992). Over the 3 years, 57% of gross photosynthesis and 85% of net photosynthesis were allocated to roots. This is consistent with the simulation results of Detling et al. (1979) who found that 65% of \(P_g\) and 80% of \(P_n\) were allocated to belowground structures. Sixty-one percent of \(P_g\) was lost in total respiration, a value close to that found by Detling et al. (1979). Root respiration represented 46% of total respiration, an intermediate value between the lowest 21% found by Bachelet (1989) and the highest 71% by Detling et al. (1979). The amount lost by aboveground respiration was 33% of \(P_g\).

Efficiency of PAR interception by green leaves was closely related to the pattern of LAI development. The maximum value was 0.41 for a LAI of 0.94. Over the simulation period, only 14% of the incident PAR was intercepted by living vegetation. The efficiency with which this intercepted PAR was converted into gross photosynthesis was 1.92 g DM (MJ IPAR\(^{-1}\)). This simulated low value was due to the effect of non-optimum temperatures, water limitation and leaf ageing. The efficiency with which the intercepted PAR was converted into aboveground net production was found to be even lower, due to the model’s high

Fig. 2. Simulated daily (a) total evaporation, (b) evaporation from soil, and (c) transpiration.
proportion of assimilate allocation to the roots, and the carbon losses due to respiration. This efficiency was 0.29 g DM (MJ IPAR)$^{-1}$ (equivalent to 0.12 g C (MJ IPAR)$^{-1}$). This value was in the lower range of those found by Paruelo et al. (1997), in 19 sites of the central grassland region of the United States. The conversion efficiencies found by Paruelo et al. (1997) varied between 0.1 g C (MJ IPAR)$^{-1}$ for the least productive sites to 0.20 g C (MJ IPAR)$^{-1}$ for the most productive sites.

Water Use Efficiency (WUE) is an interesting indicator of the efficiency with which scarce water resources are used by plants in arid or semiarid environments. WUE was defined here as the ratio of ANPP or TNPP to the total water evapotranspired or transpired during a given period of time. Most of the WUE values given in the literature for natural ecosystems were calculated as the ratio of ANPP/AET, due to the difficulty of estimating BNPP and transpiration. Values obtained for shortgrass prairies of the United States usually range between 0.2 and 0.7 g DM kg$^{-1}$ evaporated H$_2$O (e.g. Webb et al., 1978; Lauenroth, 1979; Le Houérou, 1984; Sala et al., 1988; Liang et al., 1989). The mean value obtained for the 3 years was 0.30, and when considering only the growing period, it was 0.37. These values are in the lower range of those given above. Le Houérou (1984) found that WUE tended to decrease when aridity and the rate of inefficient rain increased, and as potential evaporation increased. Thus, the climatic conditions at the Kendall site could explain the low estimates of WUE, which was related to the low transpiration/AET ratio. A sensitivity analysis of the model to changes in some parameters, showed that when the field capacity of the two upper 0–2 and 2–15 cm layers was reduced, infiltration increased, thus reducing soil evaporation,
which in turn increased the transpiration/AET ratio and consequently the WUE. This result was consistent with those found by Liang et al. (1989) and is called the inverse texture effect. Sala et al. (1988) found that when precipitation was less than 370 mm per year in North American semi-arid grasslands, sandy soils with low field capacity and low water-holding capacity were more productive than loamy soils with high water-holding capacity, while the opposite pattern occurred when precipitation was more than 370 mm.

When WUE is defined as the ratio of TNPP/AET (WUE–TNPP), an annual value of 0.76 was obtained while a value of 1.05 was found when only the growing season was considered. The values obtained by Sims and Singh (1978) over the growing season on a desert grassland range between 0.87 and 2.07.

Transpiration Use Efficiency (TUE) can be defined as the ratio of net production/transpiration. We obtained TUE–ANPP of about 1.52 g DM kg\(^{-1}\) transpired H\(_2\)O and TUE–TNPP of about 3.93 on an annual basis, or 4.37 for the growing season. The TUE–ANPP obtained was higher than that reported by Aguiar et al. (1996) (1.07 g DM kg\(^{-1}\) transpired H\(_2\)O), but similar to those of Downes (1969) who found 1.49 for grasses. The TUE–TNPP values obtained were higher than those found by Dwyer and De Garmo (1970) (2.29 g DM kg\(^{-1}\) H\(_2\)O for \(B.\) \(eriopoda\) Torr. and \(Hilaria mutica\) (Bckl.) Benth.), but lower than those found by Wright and Dobrenz (1973) for different lines of \(Eragrostis lehmanniana\) Nees (between 5.62 and 7.41 g DM kg\(^{-1}\) H\(_2\)O depending on the line).

5. Conclusions and further developments

The model presented in this paper simulates the water and carbon fluxes of a shortgrass ecosystem with a daily time step. It is driven by daily meteorological data and requires a limited number of easily available site-specific parameters. Data gathered on a grassland site in southeastern Arizona during three
consecutive years with contrasting rainfall patterns and biomass productions were used to validate the model. It was shown that the model was capable of adequately reproducing the time course of biomass, LAI, and soil water content for the three consecutive growing seasons without interruption. Furthermore, other state variables or terms of the water and carbon budgets (e.g. transpiration) which could not be directly compared to field measurements, have been compared with results of previous works carried out on similar ecosystems. This indicated an overall consistency between results of the model simulations and results of other studies.

Estimates of biomass production and evapotranspiration fluxes at a regional scale are important information for rangeland management. However, the application of simulation models for that purpose could be undermined by spatially unknown parameters such as rooting depth, or initial conditions such as root biomass, and climatic data such as rainfall, to which model simulations can be moderately to highly sensitive. At that scale, the spatial and temporal information provided by satellite sensors could prove valuable, and an assessment of the possibility of combining remote sensing data and model simulations is being carried out (Nouvellon et al., 1998, 1999).

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