

Modelling of daily fluxes of water and carbon from shortgrass steppes

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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 under-

standing 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

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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):

$$\frac{dB_{ag}}{dt} = a_a P_g + T_{ra} - R_{at} - S_a \quad (1)$$

$$\frac{dB_r}{dt} = a_r P_g - T_{ra} - R_{rt} - S_r \quad (2)$$

$$\frac{dB_{ad}}{dt} = S_a - L \quad (3)$$

where B_{ag} , B_r , and B_{ad} are living aboveground biomass, living root biomass and standing dead biomass, respectively; P_g is the daily gross photosynthesis; a_a and a_r are the photosynthate allocation partition coefficients to shoot and root compartments ($a_a + a_r = 1$); T_{ra} represents the translocation of carbohydrates from the roots to the living aboveground compartment; R_{at} and R_{rt} are total daily amounts of respiration from aboveground and root compartments, S_a and S_r represent the losses of biomass of the living shoots and roots due to senescence; and L represents the litter fall. B_{ag} , B_r , 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

$$P_g = S \varepsilon_c \varepsilon_I \varepsilon_b f_1(\Psi_1) f_2(T) \quad (4)$$

where S is the daily incoming solar radiation; ε_c the climatic efficiency (Photosynthetically Active Radiation (PAR)/ S); ε_I the efficiency of interception by green leaves (or $fPAR = \text{intercepted PAR}/PAR$); and

ε_b is the energy conversion efficiency (or g assimilated CH_2O per unit of intercepted PAR). Functions f_1 and f_2 account for the constraints imposed by water stress, leaf water potential, Ψ_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):

$$f_1(\Psi_1) = \frac{(1.64 r_{s \min} + r_m + 1.39 r_a)}{(1.64 r_{sc} + r_m + 1.39 r_a)} \quad (5)$$

where r_{sc} and $r_{s \min}$ 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 $20^\circ C$, and the ratio of the rate of transfer of CO_2 and water vapour in the canopy boundary layer, respectively. r_{sc} is calculated as a function of Ψ_1 (see below). For C_4 grasses, r_m is approximately 80 sm^{-1} (Gifford and Musgrave, 1973; Jones, 1992), and $r_{s \min}$ 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:

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

where T_{\min} and T_{opt} are the minimum and optimum temperature for gross photosynthesis of C_4 grasses, respectively $7^\circ C$ (Sauer, 1978) and $38^\circ C$ (Penning de Vries and Djitéye, 1982).

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

$$\varepsilon_I = \left[1 - e^{(-k_1 L_t)} \right] \frac{L_g}{L_t} \quad (7)$$

$$L_g = S_g B_{ag} \quad (8)$$

$$L_d = S_d B_{ad} \quad (9)$$

$$L_t = L_g + L_d \quad (10)$$

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 [$0.0105 \text{ m}^2 \text{ g}^{-1}$ and $0.0110 \text{ m}^2 \text{ g}^{-1}$, respectively (Goff, 1985)]; k_1 has been measured in a similar semi-arid grassland to be 0.58 (Nouvellon, 1999).

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

$$\varepsilon_b = \varepsilon_{b \max} f_3(\text{age}) \quad (11)$$

where $\varepsilon_{b \max}$ is the maximum energy conversion efficiency for young mature tissues, and f_3 is an empirical function representing the effect of aging on ε_b . The physiological leaf age and f_3 were calculated as in the BLUEGRAMA model (Detling et al., 1979). $\varepsilon_{b \max}$ 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_a 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:

$$r_x = \frac{B_r + T_{ar}}{B_{ag} - T_{ar}} \quad (13)$$

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 :

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

The allocation coefficient for aboveground parts is calculated as:

$$a_a = 1 - a_r \quad (16)$$

When the calculated shoot senescence exceeds a critical rate of 0.012, a_r 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 (*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) $B_r > r_x B_{ag}$.

If all these conditions are met:

$$T_{ra} = t_r B_r \quad (17)$$

where t_r 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:

$$R_{rt} = m_r f_4(T) B_r + g_r (a_r P_g) \quad (19)$$

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 Djitéye, 1982; Amthor, 1984; Ruimy 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:

$$S_a = d_a B_{ag} \quad (20)$$

$$S_r = d_r B_r \quad (21)$$

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):

$$k_r = 0.25 [1 - \exp(-0.025 R)] \quad (22)$$

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:

$$L_a = k_r B_{ad} \quad (23)$$

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 θ and water potential ψ ; 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):

$$\psi = A\theta^b \quad (24)$$

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 θ 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:

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

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

$$\Delta\theta_i = \frac{D_{i-1} - E_{si} - Q_{ci} - D_i}{z_i - z_{i-1}} \quad (26)$$

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 $\theta_i > \theta_{fci}$, where θ_{fci} is the field capacity ($\text{mm}^3 \text{mm}^{-3}$).

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_s are respectively, the cover fraction of green vegetation, dead vegetation and bare soil ($f_{vg} + f_{vd} + f_s = 1$), E_c and E_s are calculated based on Penman-Monteith equation (Monteith, 1965) as:

$$E_c = f_{vg} \frac{[sA + \rho c_p D / r_{ac}]}{[(s + \gamma(1 + r_{sc}/r_{ac}))\lambda]} \quad (27)$$

$$E_s = f_s \frac{[sA + \rho c_p D / r_{as}]}{[(s + \gamma(1 + r_{ss}/r_{as}))\lambda]} \quad (28)$$

where A is the available energy, which is the difference between net radiation R_n and soil heat flux G ; D the vapour pressure deficit of the air at a reference height above the surface; λ the latent heat of vaporisation; ρ air density; c_p the specific heat of air at constant pressure; γ the psychrometric constant and s is the slope of the saturated vapour pressure curve at the temperature of the air T_a ; r_{sc} and r_{ss} are the surface resistances for a full canopy and a bare soil, respectively; and r_{ac} and r_{as} are the corresponding aerodynamic resistances. f_{vg} and f_{vd} are calculated as a function of L_g and L_d :

$$f_{vg} = \left[1 - e^{(-k_2 L_t)} \right] \frac{L_g}{L_t} \quad (29)$$

$$f_{vd} = \left[1 - e^{(-k_2 L_t)} \right] \frac{L_d}{L_t} \quad (30)$$

The evaporation E_s is distributed between the different layers of the soil profile following an extinction coefficient which depends on soil water content, thickness and depth of each layer (Van Keulen, 1975; Rambal and Cornet, 1982).

In the model, rainfall interception by the canopy, and the subsequent evaporation of intercepted water are not considered. In shortgrass ecosystems, the amount of water intercepted by the canopy is usually limited by low aboveground biomass and percent cover, but it may not be negligible during the growing season if several rainfall events occur during the day (Thurow et al., 1987; Dunkerley and Booth, 1999). It was assumed that evaporation of intercepted water is compensated by an equivalent reduction in transpiration, so that it does not increase total evapotranspiration.

2.3.3. Estimation of available energy

The available energy A is the difference between net radiation R_n and soil heat flux G . R_n and G are estimated as follows:

$$R_n = S_n + L_n \quad (31)$$

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

$$S_n = S(1 - \alpha) \quad (32)$$

where S is the incoming short-wave radiation; and α 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).

$$L_n = -c(a_e + b_e \sqrt{e})\sigma(T_a + 273.2)^4 \quad (33)$$

where c is an adjustment coefficient for cloud cover; e is the vapour pressure in KPa; a_e and b_e are regression coefficients ($=0.34$ and -0.14 , respectively); σ is the Stefan-Boltzmann constant; and T_a is the mean air temperature in $^{\circ}\text{C}$. The coefficient of adjustment for cloud cover is given by:

$$c = a_c \left(\frac{S}{S_0} \right) + b_c \quad (34)$$

where S_0 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 $(S_n + L_n)$, and L_n 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 Ψ_1 (MPa) as:

$$r_{sc} = r_{s\min} \left[1 + \left(\frac{\Psi_1}{\Psi_{1/2}} \right)^n \right] \quad (35)$$

where $r_{s\min}$ 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):

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

where θ_1 represents the water content of the top soil 0–0.02 m layer ($\text{m}^3 \text{H}_2\text{O m}^{-3}$ soil); θ_{s1} is the soil water content at saturation ($\text{m}^3 \text{m}^{-3}$) of the ground surface layer.

The aerodynamic resistances are calculated as:

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

where z_r 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, $z_0 = 0.01$ 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 Ψ_1 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:

$$Q_i = \frac{(\Psi_{si} - \Psi_1)}{r_{spi}} \quad (38)$$

where r_{spi} and Ψ_{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 Ψ_{si} is inferred from θ_i through the soil retention curve $\Psi_s = f(\theta)$. Ψ_1 of day n is calculated from Ψ_{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 ($31^\circ 43' \text{N}$ 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. The

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 Reflectometry (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 $0.5 \text{ m} \times 1.0 \text{ m}$ quadrats, and weighing them after a 24 h 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 ± 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

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

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

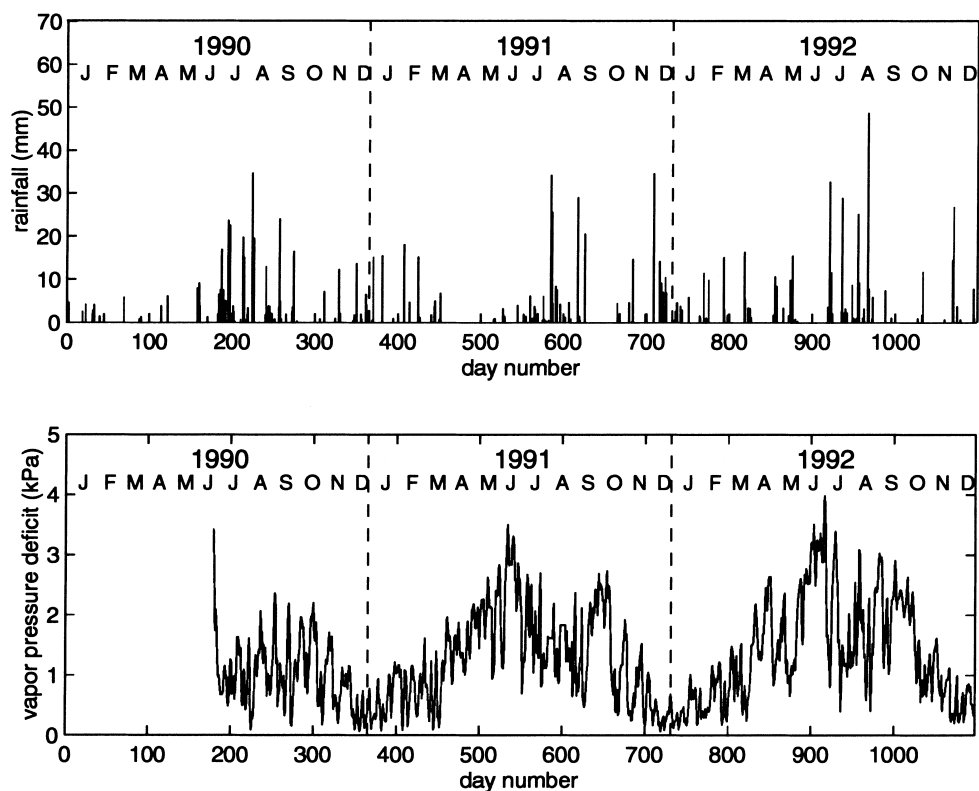


Fig. 1. Measured daily rainfall and vapour pressure deficit.

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 C_3 and C_4 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 $(\text{CH}_2\text{O})_n$)

	Units	1990 ^a	1991	1992	1990–1992
Rainfall	mm	349	369	434	1152
Global radiation	MJ	3679	7036	6916	17631
Net radiation	MJ	1688	3330	3346	8364
Total latent flux	MJ	709	837	1126	2672
Evapotranspiration	mm	289	341	459	1089
Evaporation from soil	mm	205	306	366	877
Transpiration	mm	84	35	93	212
Gross photosynthesis	g C m^{-2}	390	124	341	856
Net photosynthesis	g C m^{-2}	301	54	219	574
Total respiration	g C m^{-2}	179	135	210	525
Aboveground respiration	g C m^{-2}	90	70	122	282
Root respiration	g C m^{-2}	90	65	88	243
Allocation to roots	g C m^{-2}	264	40	185	489
TNPP	g C m^{-2}	211	–11	130	331
ANPP	g C m^{-2}	44	35	51	129
BNPP	g C m^{-2}	168	–45	80	202
Total death	g C m^{-2}	84	99	105	289
Shoot death	g C m^{-2}	46	35	51	133
Root death	g C m^{-2}	38	64	54	156
Root change	g C m^{-2}	129	–109	26	46

^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. The

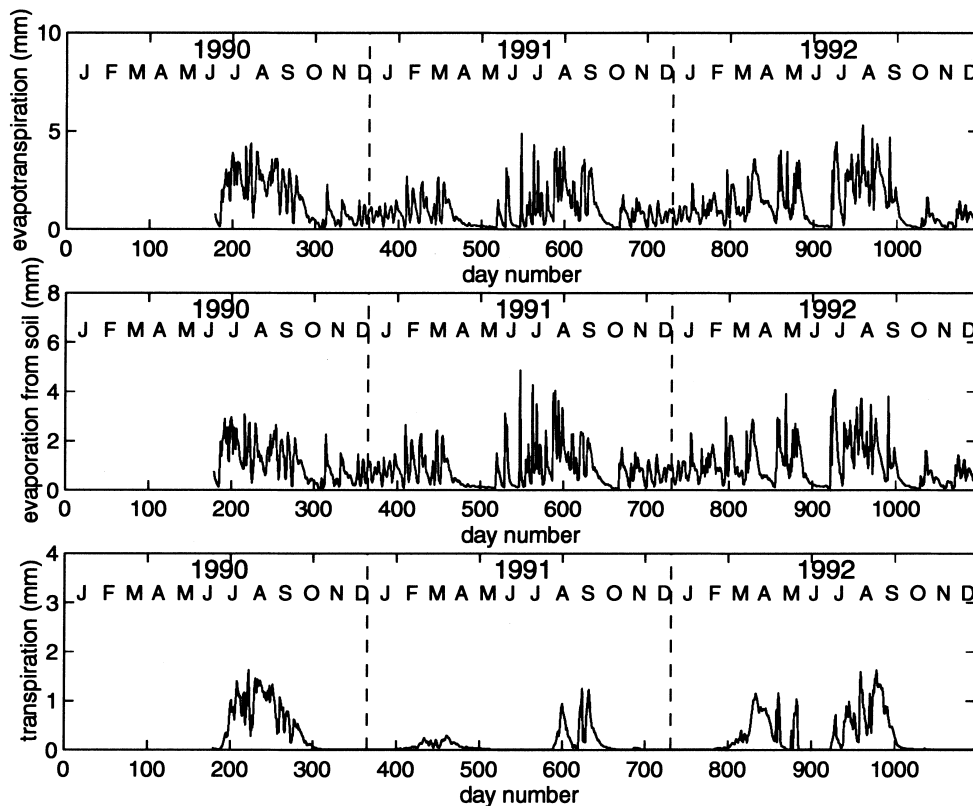


Fig. 2. Simulated daily (a) total evaporation, (b) evaporation from soil, and (c) transpiration.

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 allo-

cated 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

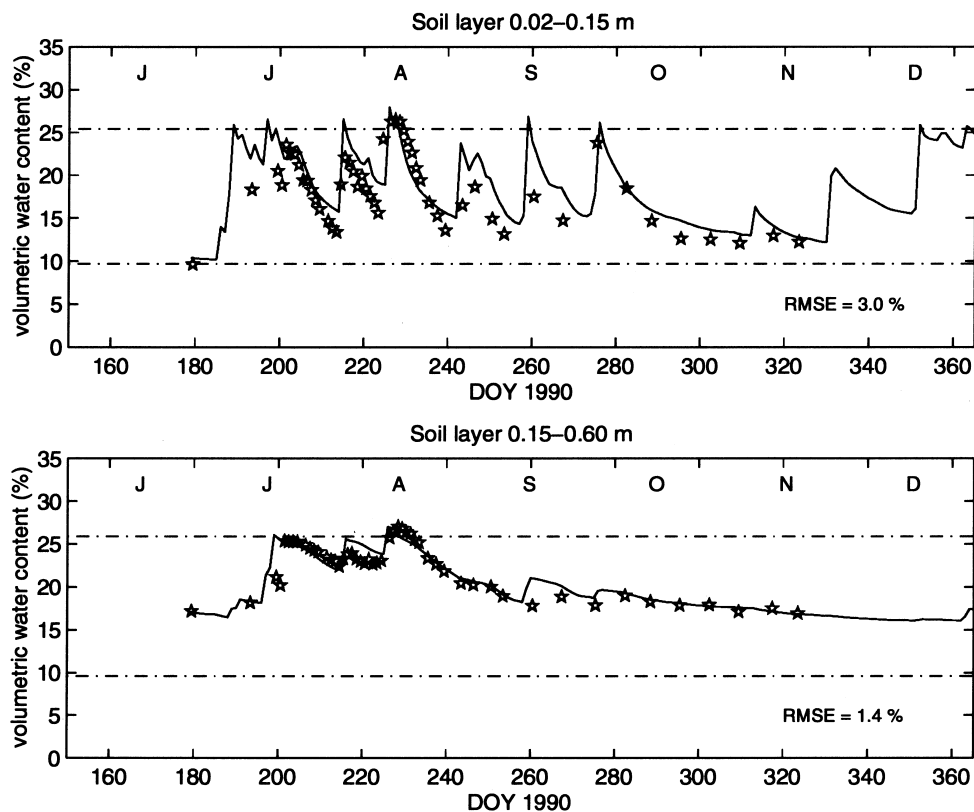


Fig. 3. Volumetric soil water content of layers 0.02–0.15 and 0.15–0.60 m. Solid lines refer to simulations and stars refer to measurements. Broken lines show field capacity and air dryness.

proportion of assimilate allocation to the roots, and the carbon losses due to respiration. This efficiency was $0.29 \text{ g DM (MJ IPAR)}^{-1}$ (equivalent to $0.12 \text{ g C (MJ IPAR)}^{-1}$). 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 $0.1 \text{ g C (MJ IPAR)}^{-1}$ for the least productive sites to $0.20 \text{ g C (MJ IPAR)}^{-1}$ 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} evapotranspired H_2O (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,

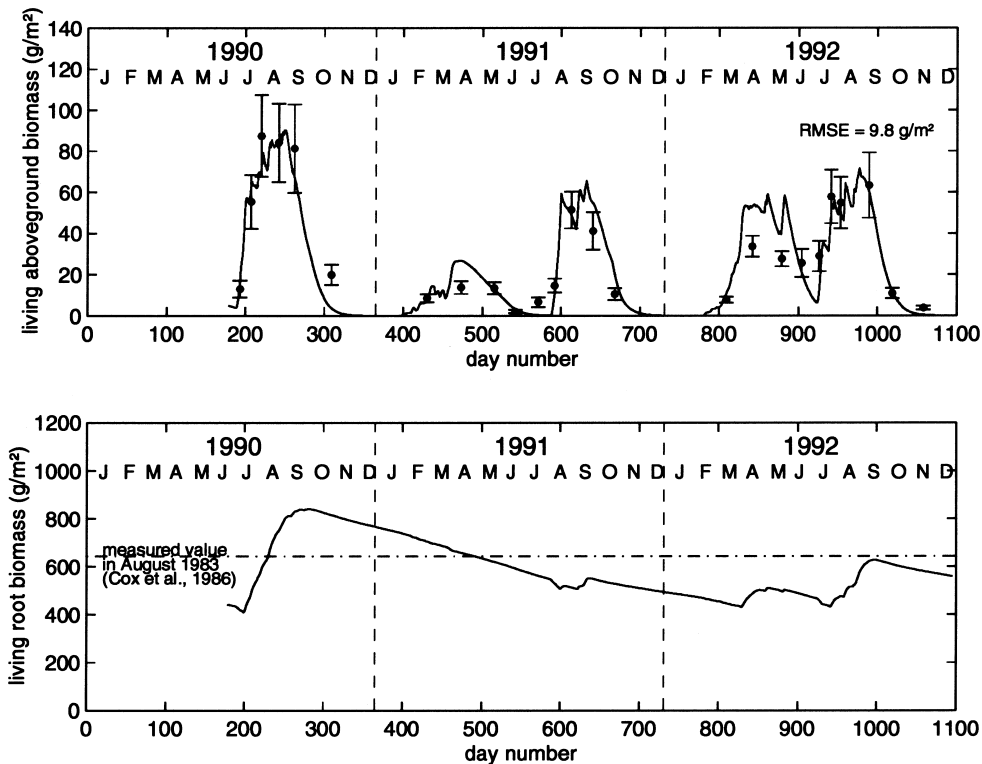


Fig. 4. Time course of simulated (a) living aboveground biomass and (b) living root biomass compared to measurements.

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 H₂O 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 H₂O), 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 H₂O 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 H₂O 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

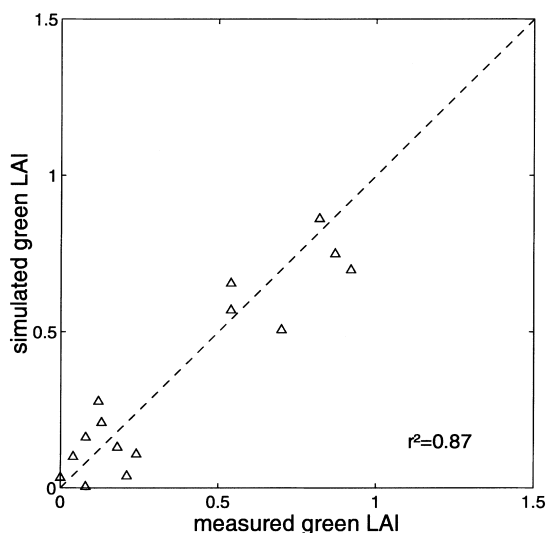


Fig. 5. Comparison of simulated and measured green LAI (1990–1991).

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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