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H. Leriche · X. LeRoux · J. Gignoux · A. Tuzet
H. Fritz · L. Abbadie · M. Loreau

Which functional processes control the short-term effect of grazing on net primary production in grasslands?

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Abstract Grazing has traditionally been viewed as detrimental to plant growth, but it has been proposed that under certain conditions, grazing may lead to compensatory or overcompensatory growth. However, comprehensive information on the relative role of the main functional processes controlling the response of net primary production (NPP) to grazing is still lacking. In this study, a modelling approach was used to quantify the relative importance of key functional processes in the response of annual canopy NPP to grazing for a West African humid grassland. The PEPSEE-grass model, which represents radiation absorption, NPP, water balance and carbon allocation, was used to compute total and aboveground NPP in response to grazing pressure. Representations of grazing and mineral nitrogen input to the canopy were simplified to focus on the vegetation processes implemented and their relative importance. Simulations were performed using a constant or resource-driven root/shoot allocation coefficient, and dependence or independence of conversion efficiency of absorbed light into dry matter on nitrogen availability. There were three main results. Firstly, the response of NPP to grazing intensity emerged as a complex result of both positive and negative, and direct and indirect effects of biomass removal on light absorption efficiency, soil water availability, grass nitrogen status and productivity, and root/shoot allocation pattern. Secondly, overcompensation was observed for aboveground NPP when assuming a nitrogen-dependent conversion efficiency and a resource-driven root/shoot allocation. Thirdly, the response of NPP to grazing was mainly controlled by the effect of plant nitrogen status on conversion efficiency and by the root/shoot allocation pattern, while the effects of improved water status and reduced light absorption were secondary.

Keywords Herbivory · Nitrogen · Overcompensation · Root/shoot allocation · Soil moisture

Introduction

Beyond consumption of a given amount of the net primary production (NPP), herbivores may have major effects on ecosystem structure and function (e.g. McNaughton et al. 1988). Grazing, which involves removal of living tissue, has primarily been considered as detrimental to plants. Many authors have represented plant-herbivore interactions by predation-like relationships (e.g. Crawley 1983), assuming that herbivory has a purely negative impact on plant growth. It is now recognised that grazing may be not detrimental, and may even be favourable for plants, in both evolutionary (see Owen and Wiegert 1976; Paige and Whitham 1987; but see Belsky et al. 1993) and functional studies.

From a functional point of view, both field and experimental results (e.g. McNaughton 1979, 1983a; Cargill and Jefferies 1984; Hik and Jefferies 1990; Biondini et al. 1998) and model simulations (e.g. Hilbert et al. 1981; Dyer et al. 1986; de Mazancourt et al. 1998) showed that NPP can be maintained (compensatory growth) or stimulated (overcompensatory growth) in response to grazing. Some authors (McNaughton 1979; Hilbert et al. 1981; Hik and Jefferies 1990) have suggested that an optimal plant removal level should occur beyond which production is reduced. The ecological significance and general-

H. Leriche (✉) · J. Gignoux · L. Abbadie · M. Loreau
Laboratoire d'Ecologie ENS, UMR 7625 CNRS,
46 rue d'Ulm, 75005 Paris, France
e-mail: eleriche@biologie.ens.fr
Tel.: +33-01-44323808, Fax: +33-01-44323885

X. LeRoux
U.A. Bioclimatologie-PIAF (INRA-Université Blaise Pascal),
Site de Crouel, 234 av. du Brezet,
63039 Clermont-Ferrand Cedex 02, France

H. Fritz
CNRS-CEBC, 79360 Beauvoir s/Niort, France

A. Tuzet
Unité de Bioclimatologie INRA, 78000 Thiverval Grignon, France

Present address: X. LeRoux
UMR 5557, CNRS/Université Claude Bernard,
Ecologie microbienne, 43 bd du 11 Novembre 1918,
69622 Villeurbanne, France

ity of these findings have recently been questioned in critical appraisals of published data (Belsky 1986, 1987; Belsky et al. 1993): overcompensatory growth has only been demonstrated under growth chamber conditions or in cultivated crops (but see McNaughton 1986; Brown and Allen 1989; DeAngelis and Huston 1992 for further discussion).

Among the many functional processes controlling NPP that are affected by grazing (see McNaughton 1983b, 1983c; Noy-Meir 1993), five major processes can be identified:

1. Modification of light availability: grazing decreases standing crop, light absorption efficiency and reduces self-shading (Jameson 1963).
2. Reduction of water loss and water stress: plant biomass reduction decreases canopy transpiration, reducing the intensity and duration of water stress for plants (Rauzi 1963; Archer and Detling 1986).
3. Accelerated or regulated nutrient recycling: plant growth may be stimulated by improved nutrient cycling induced by herbivory (Ruess 1984; Loreau 1995; McNaughton et al. 1997; Frank and Groffman 1998; de Mazancourt et al. 1999).
4. Biomass allocation: partial defoliation has a strong effect on the allocation of assimilates within the plant (e.g. Caldwell et al. 1981; Holland et al. 1992).
5. Photosynthetic rates can be increased in tissues remaining or produced after grazing (e.g. Caldwell et al. 1981; Doescher et al. 1997).

In plant-herbivore studies, the effect of grazing strongly depends on the space and time scales considered (Brown and Allen 1989). In the short term (within a growing season), the response of NPP to grazing will be determined by complex interactions between processes 1–5. For instance, the availability of light, soil water and nutrients influence the patterns of carbon allocation between roots and shoots (e.g. Davidson 1969; Brouwer 1983), whereas both nutrient and water availabilities control actual photosynthetic rates. Predicting the effect of grazing on plant relative growth rate (RGR) under given environmental conditions involves accounting for these complex interactions. Furthermore, because NPP following grazing depends on both plant RGR and biomass, the occurrence of ecophysiological processes increasing RGR after grazing does not necessarily imply a positive response of NPP to grazing (Hilbert et al. 1981).

In the last decade, the grazing optimisation hypothesis applied to individual plants or canopies at the weekly to yearly time scale was tested through experiments controlling light (McNaughton 1992), nutrient (Ruess 1984) and water availability (Simoes and Baruch 1991; Paez et al. 1995), or both nutrient and water status (McNaughton 1983c). Apart from a simulation model (Coughenour 1984; Coughenour et al. 1984) using morphological and physiological features to assess the impact of grazing on grass production, comprehensive approaches coupling major functional processes are scarce. This is a major obstacle to understanding and generalising plant functional response to grazing.

Our objective was to better understand the impact of grazing on vegetation production by simulating the response of grass NPP to plant biomass removal. We used a process-based model of African grasslands in order (1) to quantify the relative importance of key functional processes (changes in light absorption efficiency, reduction of water stress, improved canopy nitrogen status and ensuing productivity rate, changes in the pattern of root/shoot allocation) in the response of NPP to grazing, and particularly those that can lead to compensatory growth, and (2) to test the grazing optimisation hypothesis under different functional hypotheses at the canopy and annual scales for a nitrogen-poor humid grassland (Lamto, Ivory Coast).

Materials and methods

Study site

Data were collected in the Guinea savannas of the Lamto reserve (6°13′N, 5°02′W) in Ivory Coast, characterised by a dense and tall grass layer dominated by scattered isolated trees and tree clumps (Menaut and César 1979). Annual precipitation averages 1200 mm, and well-defined precipitation periods occur: a rainy season from February to November, interrupted by a short dry season in August, and a dry season in December and January. Temperatures are quite constant all year round (annual mean 27°C). Fires occur yearly in January.

Because of intense hunting pressure in the last decades, herbivore densities are low. The number of large grazers has increased recently due to hunting prohibition on the reserve area: antelope (e.g. *Kobus kob*, 0.03 individuals ha^{-1}) and buffalo (*Syncerus caffer nanus*, 0.024 ind ha^{-1}) densities both fall within the range of values found in protected areas in Western Africa (Fritz 1997).

The study focused on tropical grasslands dominated by C_4 bunchgrass species from the genera *Hyparrhenia* and *Andropogon*. *H. diplandra* (Hack.) Stapf. was the dominant grass on the study site.

Model structure and assumptions

The PEPSEE-grass model (Production, Evapotranspiration and Phenology in Savanna EcosystEms: Le Roux 1995) explicitly links the seasonal variations in soil water availability and primary production in tropical grasslands. The model includes (1) a NPP/phenology module that simulates the seasonal courses of grass biomass and necromass, and corresponding green and dead leaf area indices (LAI), (2) a water balance module that simulates changes of water availability in two soil layers, and (3) a simple plant nitrogen balance module that uses soil nitrogen uptake by the canopy as an input (Fig. 1). The depth of the upper soil layer is defined so that this layer contains 90% of root mass. The depth of the deeper soil layer corresponds to the maximum rooting depth of the vegetation. LAI controls both primary productivity and evapotranspiration rate. Water availability modulates NPP, plant transpiration and leaf mortality. NPP is also controlled by the canopy nitrogen concentration. Root/shoot allocation is a function of both plant nutrient and soil water statuses. The model is run at a daily time step.

NPP module

The Monteith (1972) parametric model is used to simulate daily total primary production, TNPP (g m^{-2} day^{-1}):

$$\mathrm{TNPP}=\varepsilon_c\, f_{\mathrm{APAR\text{-}green}}\, \varepsilon_s\, R_s \qquad (1)$$

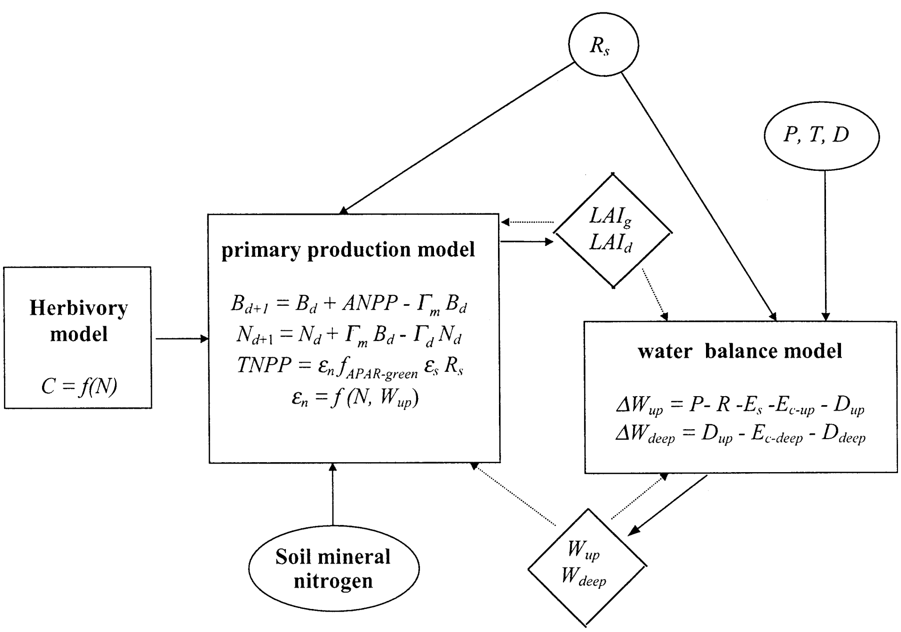

Fig. 1 Schematic representation of the PEPSEE-grass model. *Symbols* as in Table 1, *equations* are detailed in the text (Materials and methods section)

where R_s is daily total downward solar radiation (MJ m^{-2} day^{-1}), ε_s is the incident PAR (photosynthetically active radiation) to R_s ratio, $f_{\mathrm{APAR\text{-}green}}$ is the fractional absorption of PAR (APAR) by green leaves, and ε_c (the net production efficiency) is the ratio of TNPP to absorbed PAR (g dry matter MJ^{-1} APAR). Total f_{APAR} (i.e. absorption by green plus dead matter) is estimated according to the formulation of Goudrian (1977):

$$f_{\mathrm{APAR}}=0.96[1-\exp(-k_g a_g^{0.5}\,\mathrm{LAI}_g-k_d a_d^{0.5}\,\mathrm{LAI}_d)] \qquad (2)$$

where 0.96 is the asymptotic value of f_{APAR} for an infinitely thick canopy, k_g and k_d are PAR extinction coefficients for green and dead leaves, respectively, a_g and a_d are PAR absorbances of green and dead leaves, respectively, and LAI_g and LAI_d are green and dead LAIs. $f_{\mathrm{APAR\text{-}green}}$ is obtained as:

$$f_{\mathrm{APAR\text{-}green}}=[1+a_f\,(\mathrm{LAI}_d/\mathrm{LAI}_t)-b_f\,(\mathrm{LAI}_d/\mathrm{LAI}_t)^2]\,f_{\mathrm{APAR}} \qquad (3)$$

where LAI_t is total LAI. When possible, coefficients of this empirical equation should be fitted from results obtained with a radiation transfer model that can account for the vertical structure of green and dead matter within the canopy at the study site (e.g. Le Roux et al. 1997). According to published data for tropical grasslands (Cruz 1995; Le Roux et al. 1997), $\varepsilon_{\mathrm{cmax}}$ is computed as a function of the actual aboveground biomass nitrogen concentration %N:

$$\varepsilon_{\mathrm{cmax}}=a(\%\mathrm{N})+b \qquad (4)$$

where a and b are parameters. The potential conversion efficiency (i.e. the maximum value of $\varepsilon_{\mathrm{cmax}}$) is obtained when %N is maximum, i.e. when %N is that given by the potential nitrogen-biomass dilution curve (for instance 3.6% when biomass equals 100 g m^{-2} for C_4 grasses according to Cruz 1995). The actual conversion efficiency ε_c is a function of $\varepsilon_{\mathrm{cmax}}$ (i.e. for non-limiting water availability) and water availability in the upper soil layer:

$$\begin{aligned}&\text{if } W_{\mathrm{up}}<W_{\mathrm{up\text{-}t}} \text{ then } \varepsilon_c=\varepsilon_{\mathrm{cmax}}\,(W_{\mathrm{up}}-W_{\mathrm{up\text{-}wp}})/(W_{\mathrm{up\text{-}t}}-W_{\mathrm{up\text{-}wp}})\\ &\qquad\qquad\qquad\text{else } \varepsilon_c=\varepsilon_{\mathrm{cmax}}\end{aligned} \qquad (5)$$

where W_{up}, $W_{\mathrm{up\text{-}t}}$ and $W_{\mathrm{up\text{-}wp}}$ are the actual, threshold and minimum (wilting point) values of water content in the upper soil layer. As PEPSEE-grass was designed to simulate tropical grasslands, the temperature effect is ignored and only water and nitrogen stresses are assumed to restrict conversion efficiency. Other mineral deficiencies (e.g. phosphorus) are not considered.

The carbon allocation coefficient for roots (i.e. ratio of belowground to total primary production), η_r is computed according to a simple formulation (Landsberg and Waring 1997):

$$\eta_r=\alpha/[1+\beta(\varepsilon_c/\varepsilon_{\mathrm{pot}})] \qquad (6)$$

where α and β are parameters. This formulation allows η_r to depend on the relative harshness of the growing conditions, defined by the ratio $\varepsilon_c/\varepsilon_{\mathrm{pot}}$, where $\varepsilon_{\mathrm{pot}}$ is the potential ε_c (i.e. 3.31 g MJ^{-1} for C_4 grass, Cruz 1995). Equation 6 reflects the fact that the fraction of carbon allocated to roots increases when growing conditions deteriorate (e.g. drought or nutrient shortage) (Landsberg and Waring 1997) and decreases under favourable conditions. This is an empirical surrogate of the functional equilibrium approach (e.g. Brouwer 1983).

Daily aboveground production, ANPP (g m^{-2} day^{-1}), and daily belowground production, BNPP, are computed as:

$$\mathrm{BNPP}=\eta_r\mathrm{TNPP} \text{ and } \mathrm{ANPP}=(1-\eta_r)\mathrm{TNPP} \qquad (7)$$

Variations in aboveground biomass, B, and necromass, N (g m^{-2}), between days d and d+1 are simulated as:

$$B_{d+1}=B_d+\mathrm{ANPP}-\Gamma_m B_d \qquad (8)$$

$$N_{d+1}=N_d+\Gamma_m B_d-\Gamma_d N_d \qquad (9)$$

where Γ_m is the daily rate of biomass mortality (day^{-1}), and Γ_d is the daily rate of necromass disappearance (day^{-1}). In contrast to conversion efficiency or evapotranspiration rate, canopy survival can be sustained by a sufficient water availability in the deeper soil layer. Biomass mortality is not zero even in conditions of sufficient soil moisture (Littleboy and McKeon 1997) and the daily rate of biomass mortality Γ_m is a linear function of water availability of the wettest soil layer. The daily rate of necromass disappearance Γ_d is assumed constant (Le Roux 1995).

Green and dead LAIs are computed according to the stage-dependent green (SLA_g) and dead (SLA_d) specific leaf areas (in cm^2 g^{-1}) observed at Lamto (Le Roux 1995):

$$\begin{aligned}&\mathrm{SLA}_g=128-62\times[1-\exp(-0.0102\times B)]\\ &\mathrm{SLA}_d=144.2\end{aligned} \qquad (10)$$

For burned savanna sites, biomass is initialised as 10 g m^{-2} after fire occurrence (Ciret et al. 1999). This value accounts for the root-to-shoot allocation observed after fire (Le Roux et al. 1997).

Evapotranspiration module

The evapotranspiration model (Tuzet et al. 1992) uses separate treatments of soil surface evaporation and vegetation transpiration (see Appendix). Bare soil evaporation and canopy transpiration are first computed independently according to the Penman-Monteith approach. Then, actual evapotranspiration is computed as the sum of soil evaporation and canopy transpiration weighted by the fraction of net radiation intercepted by soil and green vegetation, respectively. The model was successfully tested against data from wheat and soya bean crops (Tuzet et al. 1992).

Water balance module

Water stress occurs when water content is lower than a threshold value, $W_{up\text{-}t}$, in the upper layer. Under sufficient water availability, grasses withdraw 90% of the transpired water in the upper soil layer. During water shortage, the fraction of water withdrawn from the upper soil layer compared to the total amount of water transpired, $E_{c\text{-}up}/E_c$, depends on upper soil water availability:

$$E_{c\text{-}up}/E_c=0.9(W_{up}\text{-}W_{up\text{-}wp})/(W_{up\text{-}t}\text{-}W_{up\text{-}wp}) \quad (11)$$

The remaining fraction of water is taken up in the deeper soil layer ($E_{c\text{-}deep}$). Variations of water content in the upper and deeper soil layers (W_{up} and W_{deep}, respectively) are computed as:

$$\Delta W_{up}=P\text{-}R\text{-}E_s\text{-}E_{c\text{-}up}\text{-}D_{up} \quad (12)$$

$$\Delta W_{deep}=D_{up}\text{-}E_{c\text{-}deep}\text{-}D_{deep} \quad (13)$$

where P is precipitation, R is surface runoff, and D_{up} and D_{deep} are drainage at the bottom of the upper and deeper soil layers, respectively. Drainage is assumed to occur when the water content of a soil layer is higher than its field capacity. R is computed as:

$$\text{if } P>P_0 \text{ then } R=a_R(P\text{-}P_0) \text{ else } R=0 \quad (14)$$

where P_0 is a threshold value of precipitation for runoff occurrence and a_R is a parameter.

Plant nitrogen balance module

The seasonal course of the nitrogen concentration %N in aboveground biomass is computed by a simple nitrogen balance equation where nitrogen input corresponds to nitrogen uptake by the canopy, and nitrogen loss to biomass mortality. To model nitrogen reallocation from dying biomass to remaining green biomass, leaf nitrogen concentration decreases from %N to a lower value $\%N_d$ characterising dead leaves during leaf senescence (i.e. nitrogen losses are equal to $\Gamma_m B\ \%N_d$) (Abbadie 1983). Given the absence of modules representing soil nitrogen dynamics and nitrogen uptake by roots in the current version of the model, the seasonal course of mineral nitrogen uptake by the canopy was prescribed. Because our objective was to identify key driving processes rather than predict the actual response of Lamto grasslands to grazing, and because this grassland is a steady-state ecosystem where plant growth is nitrogen-limited, the same seasonal course of nitrogen uptake by the canopy was prescribed for grazed and control treatments. No uptake occurs if nitrogen concentration in the biomass exceeds a maximum value determined by the optimal N dilution curve for C_4 grasses (Greenwood et al. 1990). This treatment of canopy nitrogen input is obviously very crude, but it was only used to test, by a sensitivity analysis, which functional processes control the short-term effect of grazing on net primary production in West African humid grasslands.

The seasonal course of nitrogen uptake by aboveground parts in the no-herbivore case during the year studied was computed by the nitrogen conservation equation applied to the grass canopy using (1) the observed seasonal courses of nitrogen concentration in necromass and biomass (Abbadie 1983), (2) the seasonal courses of biomass and necromass simulated in the control run, and (3) the observed necromass disappearance rate. Without herbivores, computed values of the nitrogen taken up by the aboveground parts strongly increased at the beginning of the vegetation cycle (Fig. 2), peaked at up to 0.01–0.015 g N m^{-2} day^{-1} during the rainy season and strongly decreased during the long dry season (after day of year, DOY, 300). The annual total nitrogen uptake was 3.3 g m^{-2}.

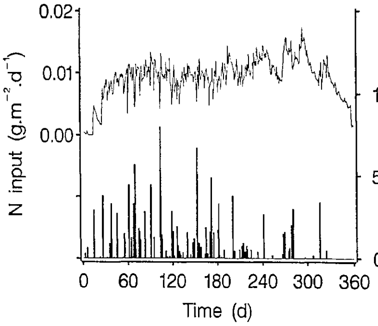

Fig. 2 Computed seasonal course of the daily amount of nitrogen uptaken by the grass aboveground parts during 1991 (*curve*) and daily precipitation pattern (*histogram*)

Herbivory module

In this study, herbivores are only considered as consumers, i.e. the effects of herbivory on the grass processes only result from “negative” herbivore effects. We expect positive effects (e.g. acceleration of the nitrogen cycle) of herbivory to further enhance any positive impact of grazing on NPP eventually simulated by our current model.

Because our main objective is to understand the key processes involved in the grass response to grazing, herbivores are modelled in a very rudimentary way. The impact of herbivores is simply represented by a daily rate of horizontally uniform biomass removal. The complex behaviour of herbivores is not considered. Herbivores are assumed to be tropical cattle (250 kg on average: Boudet 1984). Consumption is a function of grass nutritional quality (%N) and the same grazing intensity was applied throughout the year.

For low nitrogen concentration, digestion is mainly limited by the digestive capacity, the filling of the digestive tract and the higher digestion time budget because of difficulty to access to nutrients and longer digestion time (O’Reagain et al. 1996). The consumption rate, C (kg day^{-1} $herbivore^{-1}$), increases for increasing nitrogen concentration up to a threshold value of 1.04% nitrogen which corresponds to a digestible protein concentration of 25 g kg^{-1}. This value allows the grazers to fulfil their maintenance needs (0.62 kg day^{-1} $herbivore^{-1}$: Boudet 1984). The threshold value of 1.04% nitrogen is consistent with field observations in tropical savannas (Scholes and Walker 1993). For nitrogen concentrations higher than 1.04%, the daily food intake, C, is considered constant:

$$\begin{array}{l} C=\kappa\ \%N+\zeta \text{ if } \%N\leq 1.04\% \\ C=\tau \text{ otherwise} \end{array} \quad (15)$$

where κ, ζ and τ are parameters.

Herbivores are assumed to be unable to feed when grass height is lower than 20 mm (Illius and Gordon 1987), which corresponds to a threshold biomass value of 20 g m^{-2} for the Lamto savanna (Abbadie 1990). For each time step, the daily consumption rate is determined according to the individual consumption rate and the herbivore density, H (ha^{-1}).

Simulations performed

The model was parameterised for Lamto grasslands (Table 1). Simulations were performed using climate data recorded at Lamto in 1991. Nine levels of grazing intensity (H=0 to 4 ind ha^{-1}, step 0.5 ind ha^{-1})were tested. Due to the paucity of information on the responses of two processes to grazing (changes in root/shoot allocation and changes in grass conversion efficiency due to changes in grass nitrogen status), simulations were performed (1) assuming either dependence (Eq. 4) or independence (ε_{cmax}=1.26 g MJ^{-1}) of maximum production efficiency on canopy nitrogen status, and (2)

Table 1 Parameters used in the PEPSEE-grass model applied to Lamto savannas. Values are derived from Le Roux (1995), Le Roux et al. (1997) and Le Roux and Bariac (1998)

Parameter	Description	Value
a	Slope of the $\varepsilon_{\mathrm{nmax}}$-%N relationship	0.44 g MJ^{-1} %N^{-1}
a_{d}	PAR absorbance of dead leaves	0.35
a_{f}	Empirical parameter of the $f_{\mathrm{APAR\text{-}green}}$–$f_{\mathrm{APAR}}$ relationship	0.034
a_{g}	PAR absorbance of green leaves	0.78
a_{R}	Slope of the R-P relationship	0.1394
b	Intercept of the $\varepsilon_{\mathrm{nmax}}$-%N relationship	0.92 g MJ^{-1}
b_{f}	Empirical parameter of the $f_{\mathrm{APAR\text{-}green}}$–$f_{\mathrm{APAR}}$ relationship	1.034
c_{p}	Air specific heat	1012 J kg^{-1} K^{-1}
D_{v}	Diffusion coefficient of water vapour at 30 C°	2.57 10^{-5}m^{2} s^{-1}
H_{a}	Soil humidity in equilibrium with atmosphere	0.015 v/v
H_{fc}	Soil humidity at field capacity	0.1162 v/v
$k_{\mathrm{g\text{-}n}}$	Net radiation extinction coefficients for green leaves	0.7
$k_{\mathrm{d\text{-}n}}$	Net radiation extinction coefficient for dead leaves	0.4
P_0	Threshold value of precipitation for runoff occurrence	22 mm
r_{smin}	Minimum stomatal resistance	100 s m^{-1}
$W_{\mathrm{up\text{-}t}}$	Threshold water content in the upper soil layer	60 mm
$W_{\mathrm{up\text{-}wp}}$	Water content in the upper soil layer at wilting point	31 mm
α	Ratio of ANPP/TNPP when ε_{n}=0	0.9
β	Ratio of BNPP/TNPP when $\varepsilon_{\mathrm{n}}=\varepsilon_{\mathrm{pot}}$	2.5
ε_{s}	PAR to R_{s} ratio	0.485
$\varepsilon_{\mathrm{pot}}$	Potential ε_{c}	3.31 g MJ^{-1}
ζ	Intercept of the herbivory-%N relationship	1.5 kg day^{-1} herbivore^{-1}
γ	Psychrometric constant	67 Pa K^{-1}
Γd	Daily rate of necromass disappearance	0.015 day^{-1}
κ	Slope of the herbivory-%N relationship	0.964 kg day^{-1} herbivore^{-1} %N^{-1}
λ	Latent heat of vaporisation	2.43×10^{6} J kg^{-1}
ρ	Air density	1.15 kg m^{-3}
ρs	Soil bulk density	1500 kg m^{-3}
χ	Ratio of diffusion coefficients	0.25215

using either a constant (η_r=0.5) or resource-driven (Eq. 6) root/shoot allocation coefficient.

Results

Testing the four model versions without grazing

The four versions of the model adequately simulated the seasonal courses of grass canopy biomass and necromass (Fig. 3). When conversion efficiency was assumed to be nitrogen-dependent, primary productivity was higher at the beginning of the year and lower in the middle of the year than when a constant conversion efficiency was assumed. This was due to a decrease in the simulated canopy nitrogen concentration through the year (not shown). Without grazing, the simulated seasonal courses of grass canopy biomass and necromass were only weakly affected by the pattern of root/shoot allocation (i.e. constant vs. resource-driven allocation).

Effect of grazing on grass biomass and NPP

Both the nitrogen dependency of conversion efficiency and the resource dependency of root/shoot allocation had a strong effect on the response of grass biomass, total and aboveground production to grazing intensity (Fig. 4). Biomass decreased more quickly with a nitro-

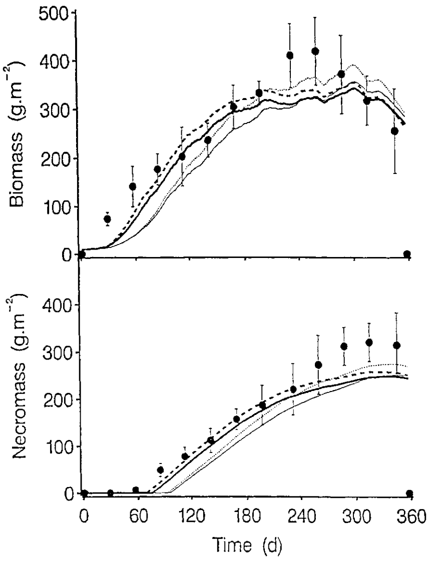

Fig. 3 Observed and simulated seasonal variations in grass biomass and necromass during 1991 for control runs (without herbivores). Simulations were performed assuming a constant conversion efficiency and a constant root/shoot ratio (*thin solid line*), a constant conversion efficiency and a resource-driven root/shoot ratio (*dotted line*), a nitrogen-dependent conversion efficiency and a constant root/shoot ratio (*thick solid line*) or a nitrogen-dependent conversion efficiency and a resource-driven root/shoot ratio (*dashed line*). Observed values (●) are presented ± the confidence interval (P=0.05)

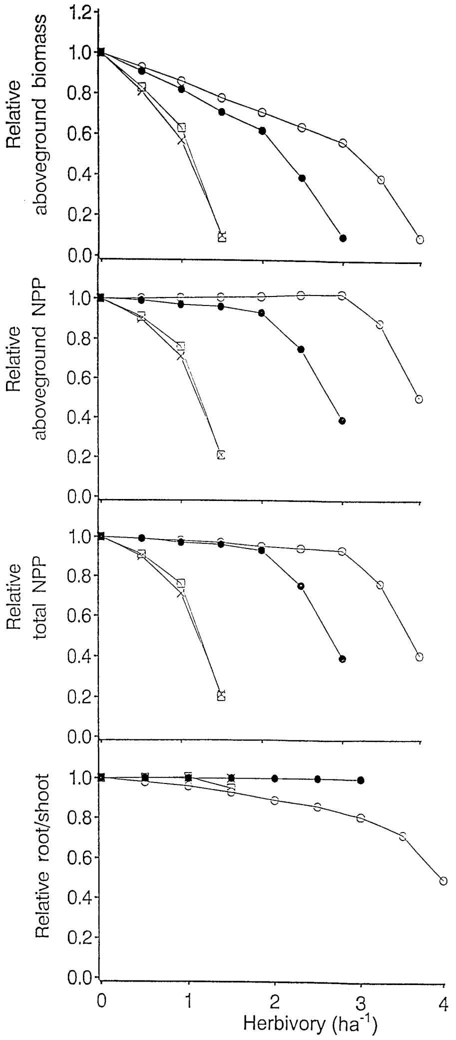

Fig. 4 Simulated response of grass biomass (mean of daily values over the year), aboveground net primary production (NPP), total NPP (mean over the same period) and the annual mean root/shoot ratio (ratio of belowground production to aboveground production) to grazing intensity for the four versions of the models (-×-×- constant conversion efficiency and constant root/shoot ratio, -□-□- constant conversion efficiency and resource-driven root/shoot ratio, -●-●- nitrogen-dependent conversion efficiency and constant root/shoot ratio, -○-○- nitrogen-dependent conversion efficiency and resource-driven root/shoot ratio). All values are normalised to values simulated without herbivory

gen-independent conversion efficiency. For a nitrogen-dependent conversion efficiency, biomass decreased more rapidly with a resource-independent allocation. The threshold value of 20 g m^{-2} was reached for H=1.5 ind ha^{-1} with a nitrogen-independent conversion efficiency, H=3 ind ha^{-1} with a nitrogen-dependent conversion efficiency and a constant root/shoot allocation coefficient, and H=4 ind ha^{-1} with a nitrogen-dependent conversion efficiency and a resource-driven root/shoot allocation coefficient (Fig. 4A).

In the nitrogen-independent conversion efficiency case, annual NPP decreased monotonically, and was only weakly affected by the pattern of root/shoot allocation

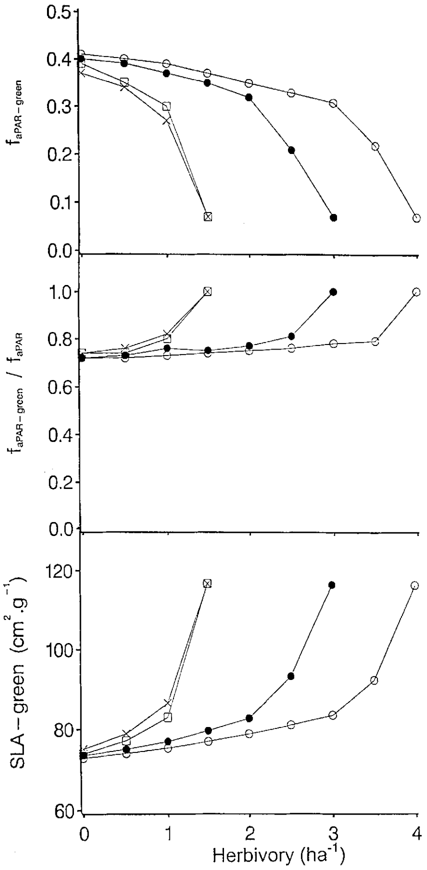

Fig. 5 Annual mean light absorption efficiency by green leaves ($f_{\mathrm{APAR\text{-}green}}$), mean ratio of light absorption by green parts to total light absortion by the canopy ($f_{\mathrm{APAR\text{-}green}}/f_{\mathrm{APAR}}$), and annual mean value of grass specific leaf area (SLA) as a function of herbivory intensity. *Symbols* as in Fig. 4

(Fig. 4). In contrast, NPP largely compensated for moderate values of grazing intensity with a nitrogen-dependent conversion efficiency. The relative decrease in NPP in response to moderate grazing was low with a constant root/shoot allocation coefficient (–6% for total and aboveground NPP for H=2 ind ha^{-1}). With a resource driven root/shoot allocation coefficient, the relative decrease in total NPP was slightly lower while a slight overcompensation was observed for aboveground NPP (+5% for H=3 ind ha^{-1}).

With a resource-dependent allocation pattern, the root/shoot production ratio decreased with increasing grazing intensity (Fig. 4). The relative change in the root/shoot production ratio was around –20% when NPP was maximised in the case of a nitrogen-dependent efficiency.

Simulated effects of grazing on light, water and nitrogen resource availability

Variations in the mean light absorption efficiency by green leaves $f_{\mathrm{APAR\text{-}green}}$ in response to grazing intensity (Fig. 5) were essentially determined by the variations in

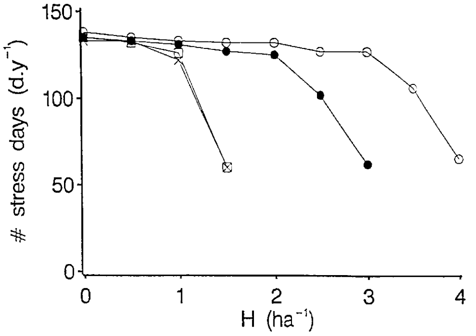

Fig. 6 Variations of the annual mean number of days when plants experienced water stress in response to herbivory intensity. *Symbols* as in Fig. 4

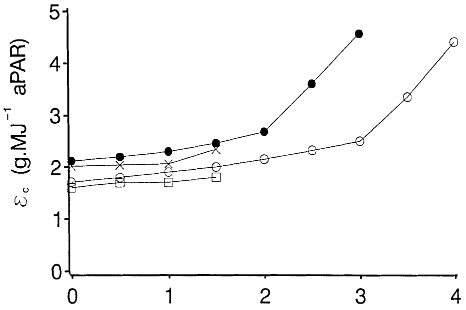

Fig. 7 Variations of the annual mean conversion efficiency ε_c of the grass canopy in response to herbivory intensity. *Symbols* as in Fig. 4

grass biomass (Fig. 4). The annual value of $f_{\mathrm{APAR\text{-}green}}$ decreased from *c*. 0.4 in control runs to 0.05 when the minimum grass biomass was reached. The annual value of the ratio of light absorption by green parts to total light absorption by the canopy was influenced by grazing intensity (Fig. 5) and increased from around 0.72 in control runs (for which the yearly necromass to biomass ratio was around 0.3, not shown) to 1.0 when the threshold value of grass biomass was reached (necromass to biomass ratio close to zero). The grass SLA increased from 74 cm^2 g^{-1} without herbivore to 116 cm^2 g^{-1} for the maximum herbivory intensity (the increase in SLA was +14% when NPP was optimized).

Soil water balance was significantly affected by grazing intensity (Fig. 6). When grazing intensity increased, (1) daily mean total evapotranspiration decreased down to *c*. 80% of its value without herbivores, (2) the soil evaporation/total evapotranspiration ratio strongly increased (from *c*. 25% without herbivore up to 80% at maximum grazing intensity), and (3) the number of water stress days was reduced to 40% of its value without herbivores (Fig. 6).

With a nitrogen-independent conversion efficiency, the mean conversion efficiency ε_c weakly increased in response to increasing herbivory (Fig. 7). In this case, the increase in ε_c was due to more favourable soil water status. With a nitrogen-dependent conversion efficiency, the mean ε_c was first slightly affected by grazing intensity and then strongly increased at high grazing rates (e.g. H=3 ind ha^{-1} for the resource driven allocation case) (Fig. 7). In this case, the increase in ε_c was due to more favourable soil water status but also to a better canopy nitrogen status. The effect of grazing on the annual value of conversion efficiency was low for grazing intensity maximising grass aboveground NPP (e.g. ε_c increased from 1.71 g MJ^{-1} APAR without herbivore to 2.5 g MJ^{-1} APAR for H=3 ind ha^{-1}). Beyond its weak effect on the mean annual value of conversion efficiency, grazing intensity affected the canopy nitrogen status and conversion efficiency during the early stages of the vegetation cycle (Fig. 8). This improved grass growth and the ability of plants to exploit the light resource at the beginning of the year, where growth is most critical for annual grass NPP.

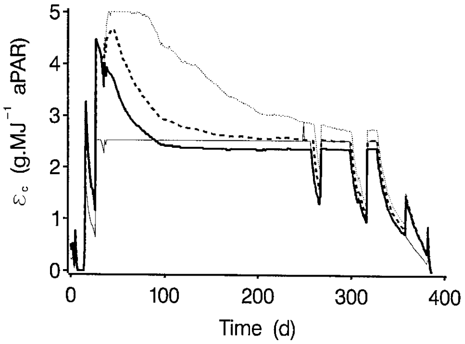

Fig. 8 Seasonal course of the conversion efficiency ε_c of the grass canopy simulated by the model assuming a nutrient-dependent conversion efficiency and a constant root/shoot allocation, for three levels of herbivory intensity (*thick solid line* H=0 ha^{-1}, *dashed line* H=1.5 ha^{-1}, *dotted line* H=2.5 ha^{-1}). For comparison, the seasonal course of the conversion efficiency simulated by the model assuming a nutrient-independent conversion efficiency and a constant root/shoot allocation is presented for the control (without herbivore) run (*thin solid line*)

Discussion

Testing the grazing optimisation hypothesis

Previous field studies testing the overcompensation hypothesis (*sensu* Belsky) for aboveground or total NPP have found either significant overcompensation (e.g. McNaughton 1979; Cargill and Jefferies 1984), compensation (e.g. Beaulieu et al. 1996; Biondini et al. 1998) or undercompensation (e.g. Rusch and Oesterheld 1997). The type of response depends on the vegetation type or ecotype, environmental conditions, and time and space scales at which grazing is considered (e.g. Brown and Allen 1989; Holland et al. 1992; Biondini et al. 1998). Our simulations showed that, in West African humid grasslands, grazing can lead to weak overcompensatory growth and a weak increase of grass aboveground NPP when conversion efficiency is assumed to be nitrogen-dependent and root/shoot allocation is assumed to be resource-driven: the maximum increase in NPP was +5% and was observed for H=3 ind ha^{-1}. When root/shoot allocation is assumed to be independent of resources, total and aboveground grass NPP nearly compensated up to H=2 ind ha^{-1}. The maximum stimulation of NPP by grazing simulated by the model under the environmental conditions studied was always lower than for previously reported stimulations (+100%, for a Serengeti grassland: McNaughton 1979; +35–70% for a subarctic salt marsh: Cargill and Jefferies 1984).

Our main objective was to quantify the relative importance of the different processes that control the ability of a grass canopy to overcompensate under moderate grazing intensity. Given the model assumptions, the aim of this paper was not to conclude whether West African humid grasslands actually overcompensate in response to moderate grazing or not. Direct field measurements are needed to draw such a conclusion.

Control of grass NPP response to grazing by light, water and nitrogen resource availability

In our model, NPP takes a simple multiplicative form:

$$\mathrm{NPP}=\varepsilon_{\mathrm{cmax}}(\%\mathrm{N})\times\mathrm{SF}\times f_{\mathrm{APAR\text{-}green}}\times\mathrm{PAR} \qquad (16)$$

The key variables influencing NPP are (1) plant nitrogen status %N, controlling conversion efficiency under non-limiting water conditions $\varepsilon_{\mathrm{cmax}}$, (2) soil water status (quantified by a stress factor SF, Eq. 11) that can restrict conversion efficiency, (3) aboveground biomass that controls the fraction $f_{\mathrm{APAR}green}$ of PAR absorbed by green leaves, and (4) root/shoot allocation pattern that determines the fraction of total NPP used for foliage growth. This simple formalism allows us to link NPP to three state variables, i.e. plant nitrogen status, soil water status and aboveground biomass, that result from the nitrogen, water and carbon budgets, respectively.

With resource-driven allocation and nitrogen-dependent conversion efficiency, the model predicted that biomass would decrease by –40% when NPP was maximised. This implied a reduction of only –20% of $f_{\mathrm{APAR}green}$, due to (1) the non-linear relationship between $f_{\mathrm{APAR}green}$ and biomass, (2) the increase of the simulated specific leaf area in response to grazing, and (3) the weak increase in $f_{\mathrm{APAR}green}/f_{\mathrm{APAR}}$. The simulated increase in SLA in response to grazing is consistent with experimental results (e.g. Simoes and Baruch 1991). The simulated increased biomass-to-necromass ratio (which explained the simulated increase in $f_{\mathrm{APAR}green}/f_{\mathrm{APAR}}$) agrees with results of field observations or experimental trials (e.g. Hamilton et al. 1998).

Another compensatory mechanism was the change in root/shoot allocation. The assumption of a resource-driven allocation had a small effect on simulation results when conversion efficiency was nitrogen independent. In this case, root/shoot allocation only responded to water availability, which had a weak influence on allocation at the annual scale. When conversion efficiency was assumed to be nitrogen-dependent, the way allocation was represented in the model had an important effect on the simulated canopy response to grazing. High NPP was maintained for herbivory intensity ranging from 2 to 3 ind ha^{-1} and overcompensation of aboveground NPP was only observed when allocation was assumed to be resource-driven (allocation depended on water and nitrogen availability). This showed that (1) changes in the root/shoot allocation pattern can have a major role in determining the response of the grass canopy to grazing, and (2) the simulated changes in allocation were mainly driven by the simulated changes in the grass nitrogen status. The simulated decrease of the root/shoot ratio in response to increasing grazing intensity is consistent with results reported for grazing-tolerant *Agropyron smithii* in an intensively grazed North American prairie (Holland et al. 1992). However, the root/shoot ratio has also been reported to remain unchanged under moderate herbivory intensity for grazing-intolerant *A. smithii* (found in uncolonized grasslands; Holland et al. 1992) and for a mixed-grass prairie (Biondini et al. 1998). Greater flexibility of allocation following defoliation was demonstrated in a grazing-tolerant bunchgrass as compared with a grazing-sensitive bunchgrass (Caldwell et al. 1981). The results of Holland et al. (1992) and Caldwell et al. (1981) support our conclusion that changes in root/shoot allocation, a species- or ecotype-dependent feature, can strongly influence the plant response to grazing.

A third compensatory mechanism is the reduction of drought intensity with increasing herbivory. Such an improved soil water status under moderate grazing is consistent with results observed during grazing experiments (Rauzi 1963; Cox and Mc Evoy 1983; Archer and Detling 1986). In our study, the reduction of transpiration largely compensated for the increase in soil evaporation (not shown). However, this improved soil water status resulted in a weak increase in conversion efficiency and in only small changes in the root/shoot ratio. The indirect effect of grazing on soil moisture was not of major importance for determining the grass response to grazing. However, our model did not account for water interception by the grass canopy and thus neglected the potential effect of changes in interception loss (Coughenour 1984). Changes in soil moisture can also strongly influence soil nitrogen dynamics (Holland and Detling 1990). Including these processes in the model is thus needed in order to better quantify the effect of the soil water status in determining plant response to herbivory.

According to simulations, the major process determining the grass response to grazing intensity was the improvement of the canopy nitrogen status that resulted in increased conversion efficiency and decreased allocation to roots. An increased nitrogen concentration in biomass in response to grazing has been reported for a Serengeti short-grass species (e.g. Ruess 1984; Hamilton et al. 1998). An increase in photosynthetic capacity (a component of the maximum conversion efficiency) has been observed in response to grazing (e.g. Doescher et al. 1997). Such an increased photosynthetic capacity is particularly important for grazing-tolerant as compared with grazing-sensitive species (Caldwell et al. 1981). Realistic simulations of the effect of grazing on grass nitrogen concentration would imply to accurately represent nitrogen uptake by plants. Nitrogen uptake by aboveground parts was predicted to increase at moderate grazing intensity for western wheatgrass (+46% up to +200% according to grazing intensity and plant population: Holland et al. 1992). However, experimental results on changes in aboveground nitrogen uptake with increasing grazing intensity are scarce (e.g. weak change in annual uptake according to Biondini et al. 1998), and no generalisation can be made. The influence of herbivores on the nitrogen cycle in the soil-plant system is complex. Herbivores can change nitrogen input to the soil (Tracy and Frank 1998) and soil net nitrogen mineralisation (e.g. Holland et al. 1992; Frank and Groffman 1998; Hamilton et al. 1998), but the mineralisation rate is also strongly controlled by actual soil moisture (Holland et al. 1992). Grazing can also affect the specific root uptake rate for nutrients (Ruess 1984). A comprehensive representation of nitrogen dynamics is thus needed to accurately simulate the grazing effect on grass production.

Importance of temporal and spatial scales for assessing the grazing effect

In our simulation approach, we used a simple representation of grazing and assumed that the same grazing intensity was applied throughout the year. The effects of the timing and length of grazing periods on canopy production will be tested in the future because of their potential influence (see Beaulieu et al. 1996; Bullock et al. 1996; Grant et al. 1996, among others). Selectivity of herbivores in their plant consumption should also be considered to refine the herbivory submodel. The patchy activity of grazers and the spatial variations in canopy characteristics (e.g. height, biomass) are important features of plant-grazer systems (e.g. Semmartin and Oesterheld 1996; Weber and Jeltsch 1998). However, the patchy functioning of grasslands in response to grazing is beyond the scope of the simple model presented here.

Conclusion

The originality of this work is to provide a comprehensive representation of the functional response of grasslands to grazing. Given the assumptions made in our model, this study did not aim at providing evidence for or against the grazing optimisation hypothesis in West African humid grasslands, but our work clearly identified (1) the changes in plant nutrient status and productivity, and (2) the response of the root/shoot allocation pattern, as the two key interacting processes controlling the response of grassland NPP to increasing grazing intensity. The first feature has already been identified from both field studies (e.g. Cargill and Jefferies 1984; Hik and Jefferies 1990; Hamilton et al. 1998) and theoretical studies (e.g. Loreau 1995; de Mazancourt et al. 1998, 1999), which supported the key role of the nitrogen cycle in the plant-soil system for determining the ability of vegetation to overcompensate under moderate grazing pressure. Studies identifying the second feature as important are scarce (but see Holland et al. 1992). We clearly show that predicting the response of grassland NPP to increasing grazing intensity requires coupling of a model simulating the functioning of the grass canopy (as the PEPSEE-grass model) to a model simulating the nitrogen dynamics in the soil-plant system (Parton et al. 1988; Gignoux et al., in press). Such an approach should accurately represent the interactions between plant functional processes (N uptake, litter or exudate inputs to the soil, dependence of grass productivity on nutrient availability, and root/shoot allocation pattern), soil microbial activities (soil organic matter dynamics and soil nutrient availability, mineralisation from urine and faeces) and soil water balance (which controls both soil and plant functioning).

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Appendix: evapotranspiration submodel

The bare soil evaporation module is based on a physical approach. The basic theory relies upon the daily mass balance of a dry surface layer of varying thickness as presented by Brisson and Perrier (1991). Just after a rainfall, soil evaporation rate λE_s (W m^{-2}) is equal to the potential soil evaporation rate λEP_s:

$$\lambda EP_s=(\Delta R_n+\rho c_p D/r_{as})/(\Delta+\gamma) \qquad \text{(A1)}$$

where λ is the latent heat of vaporisation (J kg^{-1}), Δ is the derivative of the saturation water vapor pressure with respect to temperature (Pa K^{-1}), R_n is the net radiation flux density (W m^{-2}), ρ is the air density (kg m^{-3}), c_p is the air specific heat at constant pressure (J kg^{-1} K^{-1}), D is the air water vapor pressure deficit at the reference level (Pa), and γ is the psychrometric constant (Pa K^{-1}). Computation of r_{as} is detailed by Le Roux (1995).

As soil is drying after a rainfall, cumulative actual evaporation ΣE_s (mm) is related to cumulative potential evaporation ΣEP_s (mm) (Perrier 1973; Brisson and Perrier 1991):

$$\Sigma E_s=(A^2+2A\ \Sigma EP_s)^{0.5}-A \qquad \text{(A2)}$$

$$A=(1/n)\ \Sigma A_i \qquad \text{(A3)}$$

$$A_i=[(\Delta+\gamma)/\gamma]\rho_s(H_{fc}-H_a)(D_v/\chi)r_{as} \qquad \text{(A4)}$$

where ρ_s is the soil bulk density (kg m^{-3}), H_{fc} and H_a are the relative soil humidities at field capacity and in equilibrium with atmosphere (on a dry weight basis), D_v is the diffusion coefficient of water vapour in the atmosphere (m^2 s^{-1}), χ is the ratio of diffusion coefficient within the mulch layer to diffusion coefficient in atmosphere. H_a can be estimated from soil clay content and χ is a function of air-filled porosity which can be related to soil bulk density (Brisson and Perrier 1991).

Transpiration from the vegetation canopy is a function of potential transpiration, vegetation structure, stomatal resistance and soil water availability (Tuzet et al. 1992). For sufficient water availability, canopy transpiration λE_c depends on canopy potential evaporation λEP_c (W m^{-2}):

$$\lambda EP_c=(\Delta R_n+\rho\, c_p D/r_{ac})/(\Delta+\gamma) \tag{A5}$$

where the resistance r_{ac} (s m^{-1}) is computed according to Perrier (1975) as the sum of an aerodynamic resistance and an internal resistance to heat transfer within the canopy.

For sufficient water availability ($W_{up}>W_{up\text{-}t}$), canopy transpiration depends on potential transpiration, maximum green LAI and minimum stomatal resistance r_{smin} (s m^{-1}):

$$E_c=a_0\ EP_c;\ a_0=\{1+[\gamma/(\Delta+\gamma)][r_{smin}/(r_{ac}\ LAI_{gmax})]\}^{-1} \tag{A6}$$

For conditions of limiting soil water availability, E_c depends on soil water availability in the upper soil layer in a similar way as production efficiency:

$$E_c=a_0\ EP_c\ (W_{up}-W_{up\text{-}wp})/(W_{up\text{-}t}-W_{up\text{-}wp}) \tag{A7}$$

Actual evapotranspiration E is the sum of soil evaporation and plant transpiration, weighed by the fraction of net radiation available for soil or green leaves (Tuzet et al. 1992):

$$E=E_s\ \exp(-k_{g\text{-}n}\ LAI_g-k_{d\text{-}n}\ LAI_d)+E_c[1-\exp(-k_{g\text{-}n}\ LAI_g)] \tag{A8}$$

where $k_{g\text{-}n}$ and $k_{d\text{-}n}$ are the extinction coefficients of net radiation for green and dead leaves, respectively. Net radiation intercepted by dead leaves is assumed to be dissipated as sensible heat flux.

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