Time Course of Radiation Use Efficiency in a Shortgrass Ecosystem: Consequences for Remotely Sensed Estimation of Primary Production

Yann Nouvellon,* Danny Lo Seen,* Serge Rambal,† Agnès Bégué,*
M. Susan Moran,‡ Yann Kerr,§ and Jiaguo Qi‡

A reliable estimation of primary production of terrestrial ecosystems is often a prerequisite for land survey and management, while being important also in ecological and climatological studies. At a regional scale, grassland primary production estimates are increasingly being made with the use of satellite data. In a currently used approach, regional gross, net, and aboveground net primary productivity (GPP, NPP, and ANPP) are derived from the parametric model of Monteith and are calculated as the product of the fraction of incident photosynthetically active radiation absorbed by the canopy (f_APAR) and gross, net, and aboveground net production (radiation-use) efficiencies (ε_g, ε_n, and ε_{an}); f_APAR being derived from indices calculated from satellite-measured reflectances in the red and near infrared. The accuracy and realism of the primary production values estimated by this approach therefore largely depend on an accurate estimation of ε_g, ε_n, and ε_{an}. However, data are scarce for production efficiencies of semiarid grasslands, and their time and spatial variations are poorly documented, often leading to large errors for the estimates. In this paper, a modeling approach taking into account relevant ecosystem processes and based on extensive field data was used to estimate time variations of ε_g, ε_n and ε_{an} of a shortgrass site in Arizona. These variations were explained by varia-tions in plant water stress, temperature, leaf aging, and processes such as respiration and changes in allocation pattern between above- and below-ground compartments. Over the 3 study years, averaged values of ε_g, ε_n, and ε_{an} were found to be 1.92, 0.74, and 0.29 g DM (MJ IPAR)$^{-1}$, respectively. ε_g and ε_n exhibited large interannual and seasonal variations mainly due to changes in water limitations during the growing season. Interannual variations of ε_{an} were much less important. However, for shorter periods, ε_{an} exhibited very contrasting values from regrowth to senescence. The calculation of ANPP seems less prone to errors due to environmental effects when computed on an annual basis. When estimating GPP and NPP, better results are expected if water limitations are taken into account. This could be possible through the estimation of a water-stress factor by using surface temperature or other indices derived from thermal infrared remote sensing data. The limitations due to temporally varying efficiencies, shown here for shortgrass ecosystems, are also relevant to all drought-exposed ecosystems, particularly those with abundant evergreen or perennial species. Published by Elsevier Science Inc.

* CIRAD-AMIS/Maison de la Télédétection, Montpellier, France
† CEFE-CNRS, DREAM Unit, Montpellier, France
‡ USDA-ARS-USWCL, Phoenix, AZ
§ CESBIO-CNES, Toulouse, France

Address correspondence to Yann Nouvellon, 500 rue J.F. Breton, 34093 Montpellier cedex 5, France. E-mail: yann.nouvellon@cirad.fr
Received 28 December 1998; revised 19 May 1999.

INTRODUCTION

The ability to convert canopy spectral vegetation indices into biologically meaningful variables is a key step in making use of large amounts of satellite information currently available in estimating the productivity of terrestrial ecosystems. One of the few cases where biophysical parameters can be quantitatively and remotely accessed is based on empirical correlations between seasonal pri-

mary production and the time integral of satellite-derived vegetation indices (ΣVI). This correlation was at first reported in studies such as those of Tucker et al. (1981, 1985) and Goward et al. (1985) and later confirmed as particularly attractive for studying natural semiarid grasslands (Diallo et al., 1991; Prince, 1991a; Wylie et al., 1991). These more recent studies have also shown that the linear relation obtained empirically was time and site dependent, thus limiting its potential of application. Nevertheless, the relation remains very useful because it allows satellite data to be used to make a regional-scale estimation of primary production for land management and ecological studies.

Quasi-theoretical works provide strong support for using ΣVI values to improve our knowledge of the basic processes of ecosystem productivity. A physical justification of the relation considered stems from two other relations. The first one is a direct simplification of the model proposed by Monteith (1972), which considers biomass accumulation in a vegetation canopy as the result of a succession of stages during which the available incident global radiation energy is intercepted or transformed. Primary production is then deduced as the product of global radiation and three "efficiencies": (1) ε_s, the fraction of incident solar energy useful for photosynthesis; (2) f_{APAR}, the fraction of incident photosynthetically active radiation absorbed by the canopy; and (3) ε_n, the conversion efficiency of absorbed radiation into biomass (Varlet-Grancher et al., 1982). Primary production is therefore proportional to these efficiencies and, in particular, to f_{APAR}.

The other relation is between f_{APAR} and vegetation indices derived from remote sensing data. Kumar and Monteith (1982), Asrar et al. (1984), and Sellers (1987) found that indices such as the NDVI (normalized difference vegetation index: difference between reflectances in the near infrared and red bands, normalized by their sum) and the SR (simple ratio: ratio of reflectance in the near infrared and red bands) were near-linear indicators of absorbed photosynthetic active radiation (APAR). Sellers et al. (1992) demonstrated that spectral indices from low-resolution satellites provided good area-averaged estimates of photosynthesis. The relations between NDVI and APAR, or its fraction f_{APAR}, were extensively documented at local scales and on vegetation with simple canopies such as grasses and crops (Gallo et al., 1985) and in several studies on various natural ecosystems such as coniferous or deciduous forests (Gamon et al., 1995; Law and Waring, 1994). There are now sufficient grounds for relating f_{APAR} to NDVI by a simple linear model (Ruimy et al., 1994). The relation is independent of pixel heterogeneity, plant leaf area, and variations in leaf orientation and optical properties [e.g., Pinter et al. (1983, 1985)]. On the other hand, the relation is sensitive to background, atmospheric, and bidirectional effects (Myneni

and Williams, 1994) and to the abundance of nongreen biomass (Gamon et al., 1995).

The strong relations between NDVI and f_{APAR} or even canopy structure and chemical content support the use of vegetation indices as indicators of potential photosynthetic production at landscape and larger scales. These relations provide a connection between aboveground net primary productivity (ANPP) and NDVI through the empirical model of Monteith (1972) or the process-based model of Sellers et al. (1992). However, evidence indicates that photosynthetic performances and net primary productivity (NPP) or ANPP of vegetation growing under water-limited environments cannot be predicted from NDVI alone, owing to environmental alterations in the radiation-use efficiency ε_n. Recent results illustrated uncoupling between NDVI and photosynthetic productivity due to changing ε_n (Runyon et al., 1994). The reliability of NDVI as a direct indicator of photosynthetic productivity is particularly suspect where the seasonal patterns of canopy greenness and photosynthetic activity diverge. Gamon et al. (1995) observed in evergreen canopies that NDVI failed to capture the seasonal course of leaf and canopy photosynthetic activities.

The generalization of the primary production-ΣVI relation could be justified if all the efficiencies except f_{APAR} were constant. ε_s generally varies within the range of 0.4 to 0.5, which is of the same order of magnitude of measurement errors (Varlet-Grancher et al., 1982) and can be assumed constant. The net production (radiation-use) efficiency (ε_n), however, is known to vary according to the physical environment, phenology, or species composition (Green, 1987; Hanan et al., 1995; Leblon et al., 1991; Le Roux et al., 1997; Prince, 1991b; Steinmetz et al., 1990). Experimental values for various types of vegetation were found between 0.2 and 4.8 gDM MJ^{-1} (Prince, 1991b). The accuracy and realism of the primary production values estimated by using the approach therefore depend largely on a reliable estimation of ε_n. However, data are scarce for net production efficiency of semiarid grasslands and other biomes, and its seasonal, interannual, and spatial variations are poorly documented, often leading to large errors. Although effects responsible for the variation of ε_n were identified by several authors, few provided corresponding quantitative evaluations (Potter et al., 1993, Prince et Goward, 1995).

The objective of this paper is to (1) quantify the time variations of the production efficiencies for a semiarid perennial grassland site in Arizona during three consecutive years, (2) evaluate their sensitivity to the main environmental factors, and (3) consider their implications for the estimation of primary productivity with remote sensing data. A model that simulates the main ecosystem processes and has been validated with extensive field data is used to estimate daily, seasonal, and annual, aboveground and total, net primary production efficiencies. The values obtained are compared with those found in the lit-

erature, and the main factors responsible for their variations are analyzed.

DEFINITIONS

Underlying the general term of radiation-use efficiency are a number of more specific efficiencies that differ according to whether solar energy is converted into gross, net, or aboveground net production. The notations ε_g, ε_n, and ε_{an} used by several authors will be further employed in the text. However, the intercomparison of efficiency values given in the literature is often a difficult task owing to the different methods used to measure or calculate either the numerator (production terms: GPP, NPP, ANPP) or the denominator (radiation terms: intercepted or absorbed PAR), not to mention that the time integration periods also may differ. Some definitions are therefore in order.

Gross primary productivity (GPP) is defined as the amount of photosynthates produced by gross photosynthesis over a given period of time per unit area of ground. NPP is the total photosynthetic gain (GPP) less total respiratory losses, and ANPP is the amount of carbohydrates allocated to aboveground parts of the vegetation (both through gross photosynthesis and through translocation from below-ground to aboveground parts) minus respiration from aboveground parts. NPP is therefore equal to the change in total biomass (ΔB) plus losses through senescence (D), whereas ANPP is equal to the change in aboveground biomass (ΔB_a) plus losses through death of aerial organs (D_a). Most of the estimations of ANPP or NPP used to calculate ε_n and ε_{an} are based on harvest methods with exclusion of herbivores where measurements are made at peak biomass or at different times in the growth cycle. However, as shown by several authors (Lauenroth et al., 1986; Long et al., 1989; Singh et al., 1975), the various techniques used to calculate ANPP or NPP from these measurements yield underestimations that may differ by one order of magnitude.

A distinction is generally made between intercepted PAR (IPAR) and PAR that is absorbed (APAR) by the plant canopy. Incoming PAR is only partly absorbed by the vegetation cover; the rest is either scattered back into the atmosphere or transmitted to the soil. Part of the latter is reflected back at the soil surface into the canopy and is eventually absorbed. Although absorbed PAR is the energy available for photosynthesis and is therefore needed for the calculation of the efficiencies, it cannot be easily measured. Instead, intercepted PAR, which can be obtained by measuring the difference between incident PAR and PAR reaching the soil surface, is often used. For closed canopies, the difference may not be negligible. For example, in a humid savanna grassland of leaf area index (LAI) ~3, Le Roux et al. (1997) found $f_{IPAR} = 0.92$ and $f_{APAR} = 0.81$. For sparse canopies, how-

ever, APAR and IPAR are generally close, with APAR slightly higher when the soil albedo is high (Bégué et al., 1991). Here, for the semiarid grassland under study, APAR and IPAR were assumed to be equal.

Finally, the time period over which the efficiencies are calculated should be clearly defined, because both the production terms and the radiation terms present large time variations. For example, in regard to a perennial grassland with only one growing season, NPP calculated for the growing season will be higher than NPP calculated for the whole year owing to the maintenance cost to plant tissues during nonvegetative period.

MATERIAL AND METHODS

Site Description

Efficiencies were studied for semiarid grassland at the Kendall site, which is located in the Walnut Gulch Experimental Watershed (31°43′N, 110°W) within the San Pedro basin in southeastern Arizona (the USDA-ARS Southwest Watershed Research Center). Topography consists of gently rolling hills, and elevation is about 1526 m ASL. The annual precipitation ranges from 250 to 500 mm with approximately two-thirds falling in the "monsoon season" from July to September (Osborn et al., 1972). Over the year, daily global radiation and PAR are 19.1 MJ and 9.0 MJ, respectively. Global radiation is maximum in June (26.8 MJ d^{-1}) and minimum in December (10.0 MJ d^{-1}). The mean annual temperature is about 16.7°C, and the mean monthly temperature ranges from 8 to 27°C. Relative air humidity is low throughout the year (average value = 39.5%). The mean annual wind is about 3.6 m s^{-1}.

The vegetation cover 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).

Measurements

At the Kendall site, rainfall was monitored by using automated weighing rain gauges. Other ancillary meteorological data included wind speed, solar irradiation, relative air humidity, and air temperature measured at 2 m above ground level. Net radiation also was continuously measured, as well as soil water content from time domain reflectometry probes spaced every 10 cm down to a depth of 60 cm.

Biomass and LAI were estimated at the Kendall site at 2-week to 1-month intervals during the growing seasons and at approximately 1.5-month intervals between the growth periods. Each estimation of live and dead standing biomass resulted from clipping plants within eight 0.5 m × 1.0 m quadrats and weighing them after a 24-h drying period at 70°C.
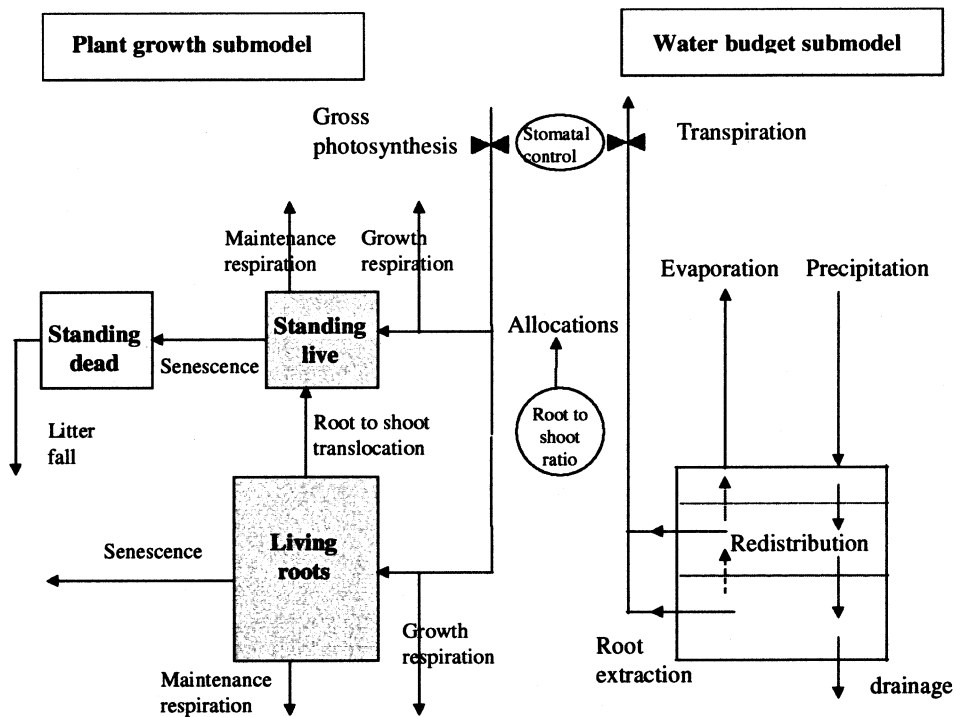
Figure 1. Schematic representation of the plant-growth and water-budget models.

Model Description

The model used in this study (Nouvellon et al., 1999) is driven by standard daily meteorological data and simulates on a daily basis the time course of biomass of green shoots, dead shoots, and living root biomass (plant-growth submodel). Transpiration, evaporation from bare soil, and soil water fluxes are simulated in a water-budget submodel. A schematic representation of the model as composed of a plant-growth submodel and a water-budget submodel is given in Figure 1.

The main processes simulated in the plant-growth submodel are photosynthesis, photosynthates partitioning between aboveground and below-ground compartments, translocation of carbohydrates from roots to shoots at the regrowth period, respiration, and senescence. Gross photosynthesis is expressed as a function of (1) PAR interception by green leaves (based on LAI); (2) a maximum energy-conversion efficiency ($\varepsilon_{g\ max}$); and (3) the depressive effects of suboptimal temperatures, water stress, and leaf aging. Allocation of photosynthates to shoots and roots and translocation of carbohydrates from roots to shoots at the regrowth depend on computed root-to-shoot ratios. The potential energy-conversion efficiency value $\varepsilon_{g\ max}$ was taken as in Charles-Edwards et al. (1986); that is, 8 g DM MJ^{-1}. The main equations used in the plant-growth submodel and from which different terms used in the present study have been deduced (GPP, NPP, ANPP, ε_g, ε_n, ε_{an}, etc.) are given in the Appendix.

The water-balance submodel uses a two-layer canopy-evaporation model in which soil profile is divided into three layers: a thin surface layer (0–2 cm), which is

supposed to participate only to soil evaporation, E$_s$, and two deeper layers (2–15 cm and 15–60 cm) corresponding to the root zone, which participate both to evaporation and to transpiration. The total evaporation from the sparse 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 the evaporation of a bare soil, according to Penman-Monteith formulations and taking into account the relative covers of green vegetation and bare soil. The leaf-water potential needed to calculate the canopy stomatal resistance is obtained iteratively by assuming that root-water uptake equals transpiration.

This model has been validated against AET (actual evapotranspiration), soil water content, biomass, and LAI values measured on several shortgrass ecosystem sites in southeastern Arizona and northeastern Sonora. The model was extensively validated with data acquired in 1990, 1991, and 1992 at the Kendall site. Very good agreements were obtained between simulated and observed aboveground biomass and LAI and between other intermediate-state variables such as soil water content in different soil layers. The time course of aboveground and below-ground biomass is given in Figure 2a and b. A more complete description of the model and its validation can be found in Nouvellon et al. (1999).

The fact that the model also simulates the daily amounts of PAR intercepted by green leaves enabled us to compute daily aboveground net production efficiency and total (aboveground + below ground) net production efficiency over different time periods.

Calculation of Factors of Efficiency Variations

In the model, plant water stress, temperature, and leaf aging are considered the main limiting factors of gross photosynthesis [see Appendix, Eqs. (1)–(6)] and are therefore the only factors assessed in the present study.

To quantify the sensitivity of an efficiency to a given environmental factor, this sensitivity must be defined with reference to a potential value that is specific for each factor. Here, the potential value of the efficiency $\varepsilon_{g\text{-pot}}$ for a given effect is obtained when that effect does not depress the efficiency. The factor is then quantified as the difference between the potential and the actual efficiency values, normalized by the potential value (see the section on Gross Primary Productivity and ε_g in the Appendix). When the efficiency values are positive (which is generally the case except occasionally for ε_n when respiration costs exceed GPP for a given time period), factor values range between 0 and 1, and lower values indicate lower effects. However, the factor values should be carefully interpreted because the effects are partly cross correlated. For example, temperature changes ε_g not only by its direct effect on GPP, but also through interaction with Ψ_f; higher temperatures result in higher air-water deficit and thereby increase water stress. Temperature also interacts with aging effects, because the rate of leaf aging is considered to increase when temperature is optimal. Nevertheless, the factors, as defined here, express the "first order," or direct, effects and offer a convenient way of comparing the different effects (1) among themselves, (2) during different periods, and (3) on the different efficiencies.

The effects of the different factors on ε_n are obtained as for ε_g. However, although the computation of the water-stress and leaf-aging factors is straightforward, that of the temperature factor needs some justification, because maintenance respiration also depends on temperature. The optimal temperature that maximizes net production is therefore not the same as the one that maximizes gross production; that is, 38°C. In fact, it changes during the growing season according to the balance between the cost of respiring tissues and the gross carbon assimilation. The potential value of ε_n, $\varepsilon_{n\text{-pot}}$, can be obtained only by considering an optimal temperature value derived each day.

RESULTS

Interannual Variations of Efficiencies and the Factors Affecting Them

Continuous simulation was done from July 1990 through December 1992. It covers three monsoon and two winter growing seasons. The cumulated rainfalls for the three monsoon seasons were 321 mm, 200 mm, and 229 mm and can be respectively considered wet, dry, and normal. The radiation-use efficiencies, together with factors such as water stress, temperature, and leaf aging that are known to influence them, are computed for (1) the monsoon seasons of 1990, 1991, and 1992, (2) the whole years 1991 and 1992, and (3) the whole simulation period from July 1990 to December 1992. The results are summarized in Table 1, with the efficiencies, factors, and
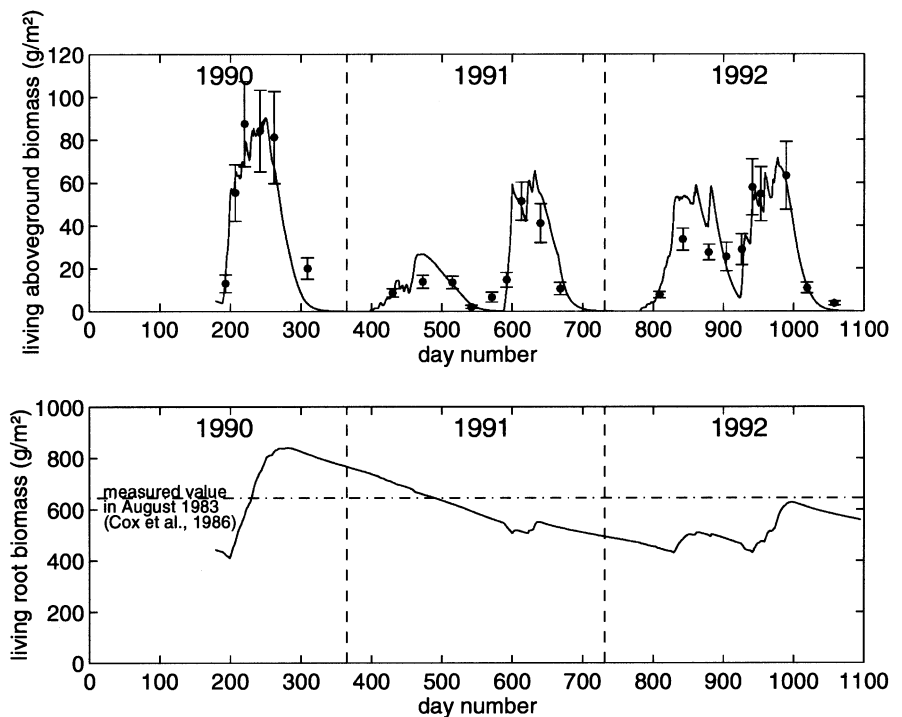

Figure 2. Time course of (top) living aboveground biomass and (bottom) living root biomass at Kendall site from June 1990 through December 1992. Solid lines show model simulations, and solid circles with error bars show biomass measurements.

Table 1. Radiation-Use Efficiencies for Summer Growing Season 1990, 1991, and 1992, and Whole Year 1991 and 1992

	(a)			(b)		(c)
	1990 (Jul–Nov)	1991 (Jul–Nov)	1992 (Jul–Nov)	1991 (Jan–Dec)	1992 (Jan–Dec)	Jul 1990– Dec 1992
Rainfall (mm)	321	200	229	385	432	1168
Incident PAR (MJ)	1402	1342	1437	3313	3230	8119
f_{APAR}	0.22	0.13	0.17	0.09	0.15	0.14
ε_g (g DM MJ^{-1})	3.12	1.45	2.22	1.01	1.73	1.92
F (water stress)	0.20	0.65	0.49	0.72	0.58	0.51
F (temperature)	0.43	0.43	0.36	0.56	0.48	0.47
F (leaf aging)	0.12	0.01	0.07	0.01	0.05	0.08
ε_n (g DM MJ^{-1})	1.72	0.20	0.93	−0.09*	0.66	0.74
F (water stress)	0.25	0.91	0.64	1.04	0.74	0.67
F (temperature)	0.31	0.75	0.32	1.16	0.51	0.49
F (leaf aging)	0.14	0.20	0.13	−1.37	0.10	0.15
Total respiration/GPP	0.45	0.86	0.58	1.09	0.62	0.61
NPP/GPP	0.55	0.14	0.42	−0.09	0.38	0.39
ε_{an} (g DM MJ^{-1})	0.35	0.32	0.27	0.28	0.26	0.29
F (water stress)	0.34	0.80	0.70	0.84	0.73	0.72
F (temperature)	0.26	0.38	0.37	0.54	0.59	0.50
F (leaf aging)	0.21	0.01	0.13	0.01	0.08	0.11
Total allocation to shoots/GPP	0.34	0.72	0.45	0.84	0.51	0.48
Aboveground respiration/total allocation to shoots	0.67	0.70	0.73	0.67	0.71	0.69
ANPP/GPP	0.11	0.22	0.12	0.28	0.15	0.15

* Negative values for ε_n occur when total respiration exceeds GPP for the given time period.

other relevant ratios relative to gross, net, and aboveground net production grouped separately.

The radiation-use efficiency for GPP ε_g is found to exhibit high interannual variations over the 3 years. Summer growing season ε_g was reduced by more than half from 1990 to 1991, whereas annual ε_g for 1991 was about eightfold less than $\varepsilon_{g\ max}$. As expected regarding rainfall amounts, the water-stress factor was particularly low in 1990 and high in 1991. Compared with the water-stress factor, the temperature factor was less variable and maintained a relatively high value. Most of the time, the leaf-aging factor was restricted to the lower range of values and became important only when the other effects were less limiting (e.g., in 1990). In addition, the effects of water and temperature stresses were higher when they were calculated for the whole year than when they were calculated for the summer growing season, because temperatures and air humidity are low during the spring growing season.

In the computation of $\_\varepsilon_n$, maintenance and growth respiration is subtracted from gross photosynthesis. ε_n therefore depends on (1) ε_g and (2) the proportion of GPP not lost through respiration. During 1991, respiration was relatively high and exceeded gross production such that ε_n was negative. This case is possible for particularly unfavorable years owing to the importance of root respiration throughout the year. When only the summer growing seasons or monsoon seasons were considered, ε_n was reduced by about 90% from 1990 to 1991. As with ε_g, large interannual variations were found, but the relative variations were much higher for net than for gross

efficiency. This finding is not surprising, because the ratio total respiration/GPP was higher for the seasons in which ε_g was lower.

Figure 3 shows the evolution of the difference between actual and optimal temperature (for net production) during the simulation period. The time course of green biomass also is given to indicate the timing of the growth cycle. It can be noted that temperature is gener-
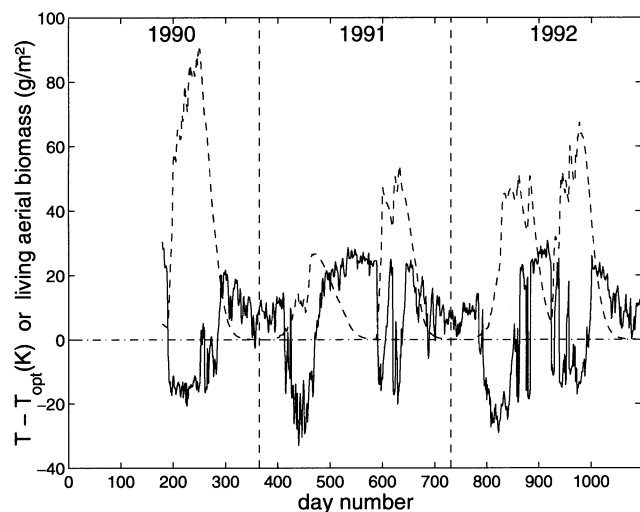

Figure 3. Difference between actual and optimal temperature $(T - T_{opt})$ for net primary production. Solid lines show temperature difference (K). The time course of living aboveground biomass (g m^{-2}) is displayed (dotted lines) to indicate the timing of the growth cycle.

ally suboptimal during the first part of a growth cycle. Temperature becomes higher than optimal as peak biomass is reached because respiration remains high while the photosynthetic capacities are reduced owing to water stress and leaf aging. Later, temperature generally remains higher than optimal, either during the senescence phase, in which photosynthetic capacities are further reduced owing to the decrease in living aerial biomass, or during the intergrowing period, in which only respiring root biomass is present.

The water-stress and leaf-aging factors are found to have a larger effect on ε_n than on ε_g because they tend to reduce GPP more than total respiration (inasmuch as only growth respiration may be changed). This finding is not necessarily the case for the temperature factor, because temperature can be responsible for large variations in both GPP and total respiration.

The variations in ε_{an} between summer growing seasons and between years were much less than those in ε_g and ε_n. ε_{an} depends on (1) ε_g; (2) the proportion of the gross photosynthesis that is allocated to the shoots, plus the amount of carbohydrates translocated from the roots to the shoots; and (3) the proportion of the carbohydrates allocated to shoots that is not lost by respiration. In spite of the fact that the water-stress factor was higher in 1991, an average value of ε_{an} was maintained. This finding can be explained by the compensation of the production deficit by higher coefficients of allocation to shoots.

Short-Term Variations of ε_g, ε_n, and ε_{an}

To better highlight the effects of both environmental variables and phenology on $\_\varepsilon_g$, ε_n, and ε_{an}, we focused our attention on the monsoon growing season, knowing that most of the annual biomass is produced during that season. The monsoon growing season was divided into three stages. The first stage (10 days) corresponds to the early regrowth when root-to-shoot translocations occur. The second stage (lasting from 44 to 61 days, depending on the year) is between the early regrowth and the last peak biomass. The last stage corresponds to senescence at the end of the growing season (from 55 to 82 days long, depending on the year).

As shown in Table 2, f_{APAR} was maximum during stage 2 because the highest LAIs were found during that stage. ε_g decreased from stage 1 to 3 owing to increasing water stress and leaf aging and decreasing temperatures. ε_n is maximum during stage 2, when relatively high values of ε_g and f_{APAR} result in an important GPP that largely compensated the loss by total respiration (GPP is more than twofold total respiration during this stage), and minimum during stage 3, when total respiration represented 90% of GPP. In stage 1, the ratio total respiration/GPP was relatively high because GPP was limited by low f_{APAR}, and total respiration was high owing to root maintenance

respiration and important growth respiration during the transformation of carbohydrates coming from the roots into new leaf and stem tissues. The effects of water stress and leaf aging remained fairly stable during stages 1 and 2 and increased drastically during the senescence phase. The high value of the temperature factor during stage 3 was due to the fact that temperature was mostly higher than optimal. ε_{an} was maximum during stage 1 owing to the high value of ε_g and root-to-shoot translocations. ε_{an} was much lower during stage 2 because 65% of the GPP was exported to the roots during this stage, and, on the 35% remaining for shoots, 66% was lost by respiration. ε_{an} was negative during stage 3, because the small amount of assimilates allocated to the shoots (resulting from low ε_g and high allocation coefficient to the roots) was less than the respiration of the aboveground senescing tissues.

DISCUSSION

Large interannual and seasonal variations were found for ε_g. Its average value for the period from June 1990 through December 1992 was about 1.92 g DM (MJ APAR)$^{-1}$. This value was lower than the one used by Ruimy (1995) [2.45 g DM (MJ APAR)$^{-1}$] for all terrestrial biomes, when computing annual global GPP. However, the latter value was close to the average ε_g that we observed for the summer growing season [2.48 g DM (MJ APAR)$^{-1}$]. Given the large variations of ε_g observed, even for year averages for the same biome, the use of one constant value to estimate GPP seems inappropriate.

Most of the interannual variations in ε_g can be explained by water limitations. The effect of leaf age does not appear very important on an annual basis, owing to the fact that, when age reduced photosynthetic capacity, the other two factors also were generally limiting. At the end of the growing season, temperatures largely decreased to values lower than optimum and the soil water availability was low. The age effect could therefore be increased for years with a wetter and warmer end of season. After the respective effects of the different factors on ε_g are taken into consideration, it can be concluded that GPP can be estimated on an annual basis if water limitations are correctly taken into account. For periods shorter than the growing season, temperature and leaf-aging effects may become determining in different stages, which is probably the case for other ecosystems found in latitudes farther north, where cold temperatures are common.

It should be noted that annual ε_n can be negative for years with low GPP (e.g., in 1991), owing to the important losses of carbon from root respiration throughout the year. The mean value of ε_n obtained for the 3 years was 0.74 g DM (MJ APAR)$^{-1}$. In comparison, that value is higher than the one derived from the Carnegie, Ames, Stanford Approach (CASA) for perennial grasslands

Table 2. Radiation-Use Efficiencies for Three Main Stages in the Summer Growing Seasons

	Stage 1: First 10 Days of Growing Seasons 90–92	Stage 2: Day 11 to Last Peak Biomass	Stage 3: Last Peak Biomass to End of Growing Season	Entire Monsoon Growing Seasons 90–92
Rainfall (mm)	102	354	110	566
Number of days	30	125	195	350
Incident PAR (MJ)	351	1283	1623	3256
f_{APAR}	0.11	0.31	0.17	0.22
ε_g (g DM MJ^{-1})	3.79	3.26	1.16	2.48
F (water stress)	0.27	0.31	0.63	0.40
F (temperature)	0.36	0.41	0.43	0.41
F (leaf aging)	0.01	0.02	0.31	0.09
ε_n (g DM MJ^{-1})	1.57	1.90	0.12	1.20
F (water stress)	0.42	0.36	0.93	0.51
F (temperature)	0.43	0.29	0.63	0.33
F (leaf aging)	0.00	0.01	0.76	0.12
Total respiration/GPP	0.59	0.42	0.90	0.52
NPP/GPP	0.42	0.59	0.11	0.48
ε_{an} (g DM MJ^{-1})	3.41	0.39	-0.20^*	0.33
F (water stress)	0.24	0.55	1.43	0.64
F (temperature)	0.59	0.42	-0.83	0.59
F (leaf aging)	0.00	0.05	-1.33	0.15
Total allocation to shoots/GPP	1.37	0.35	0.30	0.43
Aboveground respiration/total allocation to shoots	0.34	0.66	1.57	0.69
ANPP/GPP	0.90	0.12	-0.17	0.13

* Negative values for ε_{an} occur when aboveground respiration exceeds total allocation to aboveground parts for the given time period.

(Field, 1995) [0.229 g C (MJ APAR)$^{-1}$, which corresponds to about 0.57 g DM (MJ APAR)$^{-1}$] but much less than the value used by Ruimy et al. (1994) for such ecosystems [1.26 g DM (MJ APAR)$^{-1}$]. Large interannual variations in ε_n values were found. Similar variations were also reported for other biomes (Running and Hunt, 1992).

Although NPP is generally the estimation sought, it is often obtained with more difficulty, owing to the necessity to take into account autotrophic respiration. In the present study, we found that the effects of water stress on ε_n were amplified compared with ε_g. This amplification resulted in a much higher variation in ε_n values owing to environmental factors. For the estimation of annual NPP, it is therefore even more important to take into account water limitations, because proportionally larger errors can be made. This also holds for shorter periods, when it is also necessary to consider the important variations in the ratio total respiration/GPP.

The mean value obtained for the ε_{an} [0.29 g DM (MJ APAR)$^{-1}$] is in the lower range of the value found by Paruelo et al. (1997) in 19 sites of the grassland region of the central United States. The conversion efficiencies found by Paruelo et al. (1997) varied between 0.1 g C (MJ APAR)$^{-1}$ [0.25 g DM (MJ APAR)$^{-1}$] for the least productive sites and 0.20 g C (MJ APAR)$^{-1}$ [0.5 g DM (MJ APAR)$^{-1}$] for the most productive sites. Our low observed values are found to result from the high proportion of GPP that is allocated not to the shoots but to the roots and to the high rate of aboveground respiration

due to high temperatures. For the 3 years, the net exportations to the roots (allocation to the roots minus translocation from the roots to the shoots) constituted 52% of the GPP and the aboveground respiration constituted, on an annual basis, 69% of the carbohydrate amount allocated to the shoots.

The ε_{an} values observed here for semiarid perennial grasslands are much lower than those observed for semiarid annual grasslands or for humid perennial grasslands. In the Sahel, annual grassland values close to 1 g DM (MJ APAR)$^{-1}$ are often given in the literature [e.g., the mean values given by Mougin et al. (1995) and Hanan et al. (1995) were respectively 1.02 g DM (MJ IPAR)$^{-1}$ and 0.81 g DM (MJ APAR)$^{-1}$]. Values close to 1 g DM (MJ APAR)$^{-1}$ are also found for humid perennial Savanna [e.g., Le Roux et al. (1997) found 1.02 g DM (MJ APAR)$^{-1}$ in an African humid Savanna]. High differences in the proportion of assimilate allocated to the roots throughout the growing season may explain these differences. Several studies showed that, in general, perennial grasses allocate more assimilates to roots than do annuals (Ryle, 1970).

Interannual variations in ε_{an} were much less important than those in ε_g and ε_n. If this tendency is confirmed, it would imply that the estimation of ANPP on an annual basis could be carried out with fewer errors. For periods shorter than a growing season, ε_{an} exhibits very contrasting values from regrowth to senescence, and the component that should not be overlooked is the allocation term. In spite of several studies reporting the impor-
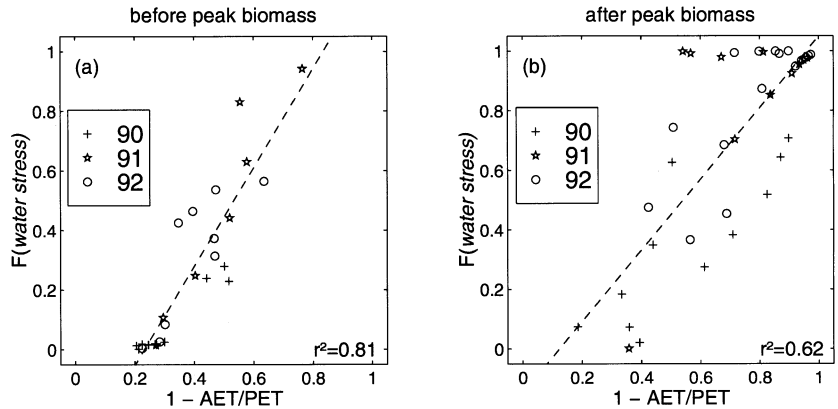
Figure 4. Comparison of *F*(water stress) and 1 − (AET/PET), where AET is actual evapotranspiration and PET is potential evapotranspiration. Each value was calculated for a 5-day period in the monsoon seasons of 1990–1992. Values corresponding to periods (a) before and (b) after peak biomass.

tance of this component in determining growth (Körner, 1991), not enough emphasis has been put on correctly taking it into account in the calculation of ANPP.

Toward a Remotely Sensed Estimation of the Water-Stress Factor

In water-limited environments, plant and canopy productivity have been linearly related to the ratio of AET/PET (actual evapotranspiration/potential evapotranspiration) for a long time (De Wit, 1958). Relations of this type have been applied at time scales ranging from the growing season to the whole year and have proved useful in various locations and particularly in grassland ecosystems for a large range of rainfall regimes (Le Houérou and Hoste, 1977). Because total rainfall gives a fairly good estimation of AET in arid and semiarid environments with low rainfall amounts, a method based on such relations is simple and easily applicable (Le Houérou, 1984). However, the same limits of applicability imposed on methods based on radiation-use efficiency hold here, in the sense that the relations also are site and time scale dependent (Deshmukh, 1984; Floret et al., 1982).

For the estimation of global NPP, studies based on radiation-use efficiency have used empirical relations in an attempt to take into account the effect of water limitation on productivity (Potter et al., 1993, Prince and Goward, 1995). In this section, we investigate how the water-stress factor, *F*(water stress), defined earlier, relate to AET/PET to verify that such an approach is justified. The water-stress factor on ε_g and 1 − (AET/PET) were calculated for 5-day periods during the monsoon seasons of 1990–1992 and plotted in Figure 4. Values corresponding to periods before and after peak biomass are plotted separately in Figure 4a and b, respectively.

Although the three seasons had contrasting rainfall supplies, a linear relation is obtained between *F*(water stress) and 1 − (AET/PET) before peak biomass. It should be noted, however, that the range of values for the three seasons differs, with a larger range for the drier season (1991), and that *F*(water stress) displays a larger range of values than does 1 − (AET/PET) (about 0–0.9

and 0.2–0.8, respectively). After peak biomass, the relation is less clear, although a similar trend is observed.

The existence of a simple linear relation between *F*(water stress) and 1 − (AET/PET) before peak biomass implies that, if an estimation of AET is available, it is possible to correct a large part of the effect of water stress on ε_g. Remotely sensed estimation of AET is another field where important progress has been made in the past 20 years (Jackson et al., 1977; Moran and Jackson, 1991; Moran et al., 1996; Seguin and Itier, 1983; Seguin et al., 1989). The results of the present study suggest that the estimation of GPP based on visible/near infrared satellite data could be improved when combined with thermal infrared data using a simple linear relation between *F*(water stress) and 1 − (AET/PET). The estimation of NPP also could be improved if it is deduced from the corrected GPP, because the maintenance respiration term is independent of water stress and growth respiration can be estimated as a fixed percentage of GPP (Ruimy et al., 1996).

Besides thermal infrared remote sensing, several recent studies suggest that hyperspectral and radar remote sensing may prove to be powerful tools for tracking canopy water status and the effect of water stress on ε_g. Peñuelas et al. (1993, 1997) found that high spectral resolution, ground-level measurements in the 950–970-nm region, and a water absorption band were good indicators of changes in relative plant water content, leaf water potential, and photosynthetic rates. Investigations focusing on other water absorption bands obtained similar results, and the potential of imaging spectroscopy for estimating spatial and temporal changes in plant water status in a wide range of ecosystems was demonstrated by several studies using airbone visible/infrared imaging spectrometer (AVIRIS) data [e.g., Gao and Goetz (1995), Green et al. (1995), Roberts et al. (1997), Ustin et al. (1998), and Gamon and Qiu (1999)]. This technique is particularly full of promise in drought-prone ecosystems such as arid, semiarid, and Mediterranean areas. Radar remote sensing is another potential source of information for monitoring changes in plant and soil water content

or status. The latter are known to cause a large change in radar backscatter (Dubois et al., 1995; Schmullius and Furrer, 1992). Recent works reported significant relations between radar backscatter and biophysical properties of temperate perennial grassland (Hill et al., 1999) and suggest that future satellite-borne multispectral syntheticaperture radar (SAR) sensors have real potential in grassland monitoring applications.

CONCLUSION

The estimation of GPP or NPP for semiarid perennial grasslands with the use of only vegetation indices derived from remote sensing data and a fixed efficiency value is inaccurate because of the temporal variations in the efficiencies. This is true even on an annual basis. The calculation of ANPP seems less prone to errors due to environmental effects when computed on an annual basis, whereas, for periods shorter than the growing season, the computation of either GPP, NPP, or ANPP is delicate. Although these limitations have been shown here for shortgrass ecosystems, they are also relevant to all drought-exposed ecosystems, particularly those with abundant evergreen or perennial species.

The modeling approach used in this study also showed that water stress was responsible for a large part of the variations in ε_g. Better results are therefore expected if water limitations are taken into account. A near linear relation was found between the water-stress factor and AET/PET before peak biomass. This relation makes possible an estimation of the water-stress factor by using surface temperature or other indices derived from thermal infrared remote sensing data and the subsequent improvement of the GPP and NPP estimations. Besides thermal infrared, other sources of information such as hyperspectral or radar remote sensing show strong potential in tracking changes in plant water status. It is suggested that they could also be used to improve the GPP and NPP estimations.

APPENDIX: EQUATIONS USED TO CALCULATE EFFICIENCIES AND THEIR SENSITIVITY TO ENVIRONMENTAL FACTORS

A description of the model used and its validation can be found in Nouvellon et al. (1999). The parts of the

model that are of particular interest in the present study, as well as the equations used to calculate the different efficiencies and how they are influenced by external factors, are given in this appendix.

Photosynthesis

The plant-growth submodel runs with a daily time step in which gross photosynthesis is expressed as a function of (1) PAR interception by green leaves (based on LAI), (2) a maximum energy-conversion efficiency ($\varepsilon_{g\,max}$), and (3) the depressive effects of suboptimal temperatures, water stress, and leaf aging:

$$P_g = PAR\, f_{APAR}\, \varepsilon_{g\,max}\, f_1(\Psi_f) f_2(T) f_3(\text{age}) \qquad (1)$$

PAR used in the model simulations was estimated as a fixed fraction (0.47) of standard daily incoming solar radiation measurements. The fraction of absorbed PAR (f_{APAR}) was simulated daily by using an empirical relation with LAI ($f_{APAR} = 1 - e^{-k.LAI}$). The coefficient k (0.58) was estimated by using ground measurements of f_{APAR} and LAI made at different periods in the growth cycles. The three depressive effects are written as follows:

$$f_1(\Psi_f) = \frac{1.64 r_{s\,min} + r_m + 1.39 r_a}{1.64 r_{sc} + r_m + 1.39 r_a} \qquad (2)$$

where

$$r_{sc} = r_{s\,min}\left[1 + \left(\frac{\Psi_f}{\Psi_{1/2}}\right)^n\right] \qquad (3)$$

and $r_{s\,min}$, r_{sc}, r_m, and r_a (s m^{-1}) are respectively the minimun and current canopy stomatal resistance to water vapor, the mesophyll, and the canopy boundary layer resistance to water vapor. Ψ_f and $\Psi_{1/2}$ are leaf water potential, current and at 50% stomatal closure (MPa), and n is an empirical shape parameter (Rambal and Cornet, 1982).

$$f_2(T) = \begin{cases} 0 & \text{if } T_a \leq T_{min} \\ 1 - \dfrac{T_{opt} - T}{T_{opt} - T_{min}} & \text{if } T_{min} < T_a < T_{opt}, \\ 1 & \text{if } T_a \geq T_{opt} \end{cases} \qquad (4)$$

where T_{opt} and T_{min} are the optimum and minimum temperatures for gross photosynthesis of C4 grasses.

$$f_3(\text{age}) = \begin{cases} 0 & \text{if age} > 50 \\ 1 - \dfrac{\text{age} - 15}{35} & \text{if } 15 < \text{age} \leq 50, \\ 1 & \text{if age} \leq 15 \end{cases} \qquad (5)$$

where age (days) is calculated as

$$\text{age}_d = \frac{(\text{age}_{d-1} + f_1(\Psi_f) f_2(T)) B_{d-1}}{B_d}, \qquad (6)$$

where age_d and B_d are effective physiological age and green biomass on day d [adapted from Detling et al. (1979)].

Gross Primary Productivity (GPP) and ε_g

GPP is obtained as the time integral of gross photosynthesis:

$$\text{GPP}=\sum_{first\_day}^{last\_day}\text{PAR}\,f_{\text{APAR}}\varepsilon_{g\,\max}f_1(\Psi_f)f_2(T)f_3(\text{age}),\qquad(7)$$

where [*first_day*, *last_day*] is equal to [1, 365] for annual GPP. Because GPP is a rate of production (of photosynthates through gross photosynthesis), it is expressed per unit time that is equal to the period of integration (e.g., $\text{gDM m}^{-2}\text{ year}^{-1}$).

ε_g for the same period is given by

$$\varepsilon_g=\frac{\text{GPP}}{\displaystyle\sum_{first\_day}^{last\_day}\text{PAR}\,f_{\text{APAR}}}.\qquad(8)$$

The effects of water stress, temperature, and leaf aging are assessed with the help of factors computed as the difference between the potential and actual efficiency values, normalized with the potential value. For example, the temperature factor is obtained as follows:

$$F(\text{temperature})=1-\frac{\varepsilon_g}{\varepsilon_{g\_pot}},\qquad(9)$$

with the potential value of the efficiency computed by using $f_2(T)=1$; that is;

$$\varepsilon_{g\_pot}=\frac{\displaystyle\sum_{first\_day}^{last\_day}\text{PAR}\,f_{\text{APAR}}\,\varepsilon_{g\,\max}f_1(\Psi_f)\,f_3(\text{age})}{\displaystyle\sum_{first\_day}^{last\_day}\text{PAR}\,f_{\text{APAR}}}.\qquad(10)$$

Net Primary Productivity (NPP) and ε_n

NPP is obtained from the gross primary productivity by subtracting maintenance and growth respiration:

$$\text{NPP}=\sum_{first\_day}^{last\_day}[\text{PAR}\,f_{\text{APAR}}\,\varepsilon_{g\,\max}f_1(\Psi_f)f_2(T)f_3(\text{age})$$
$$-R_{at}-R_{rt}],\qquad(11)$$

where R_{at} and R_{rt} are aboveground and root total respiration. The same time integration periods apply as for GPP.

ε_n for the same period is given by

$$\varepsilon_n=\frac{\text{NPP}}{\displaystyle\sum_{first\_day}^{last\_day}\text{PAR}\,f_{\text{APAR}}}.\qquad(12)$$

The effects of water stress and age on ε_n are computed as for ε_g. But, for temperature, which has an effect both on gross photosynthesis and maintenance respiration, the potential efficiency value is not given for a fixed optimal temperature throughout the year. For this reason, an optimal temperature is calculated every day so as to maximize daily net primary production. The daily values are then used in the time integration to obtain ε_{n_pot}.

Aboveground Net Primary Productivity (ANPP) and ε_{an}

For the computation of ANPP, it is necessary to take into account the allocation of assimilates between aboveground and below-ground compartments as well as translocation from roots to shoots:

$$\text{ANPP}=\sum_{first\_day}^{last\_day}[\text{PAR}\,f_{\text{APAR}}\varepsilon_{g\,\max}f_1(\Psi_f)f_2(\text{T})f_3(\text{age})a_a$$
$$+\text{TR}_{ra}-R_{at}],\qquad(13)$$

where a_a is the allocation coefficient for aboveground parts and TR_{ra} is the translocation from root to shoots.

ε_{an} for the same period is given by

$$\varepsilon_{an}=\frac{\text{ANPP}}{\displaystyle\sum_{first\_day}^{last\_day}\text{PAR}\,f_{\text{APAR}}}.\qquad(14)$$

The effects of water stress, temperature, and age on ε_{an} are computed as for ε_n.

REFERENCES

Asrar, G., Fuchs, M., Kanemasu, E. T., and Hatfield, J. L. (1984), Estimating absorbed photosynthetically active radiation and leaf area index from spectral reflectance in wheat. *Agron. J.* 76:300–306.

Bégué, A., Desprat, J. F., Imbernon, J., and Baret, F. (1991), Radiation use efficiency of pearl millet in the Sahelian zone. *Agric. For. Meteorol.* 56:93–110.

Charles-Edwards, D. A., Doley, D., and Rimmington, G. M. (1986), *Modeling Plant Growth and Developement.* Academic Press, Orlando, FL.

Cox, J. R., Frasier, G. W., and Renard, K. G. (1986), Biomass distribution at grassland and shrubland sites. *Rangelands* 8(2):67–68.

Deshmukh, I. K. (1984), A common relationship between precipitation and grassland peak biomass for East and southern Africa. *Afr. J. Ecol.* 22:181–186.

Detling, J. K, Parton, W. J., and Hunt, H. W. (1979), A simulation model of *Bouteloua gracilis* biomass dynamics on the North American shortgrass prairie. *Oecologia* 38:167–191.

De Wit, C. T. (1984), Transpiration and crop yields. *Versl. Landbouwkd. Onderz.* 64:1–88.

Diallo, O., Diouf, A., Hanan, N. P., Ndiaye, A., and Prévost, Y. (1991), AVHRR monitoring of savanna primary production in Senegal, West Africa: 1987–1988. *Int. J. Remote Sens.* 12:1259–1279.

Dubois, P., van Zyl, J., and Engman, T. (1995), Measuring soil moisture with imaging radars. *IEEE Trans. Geosci. Remote Sens.* 33:915–926.

Field, C. B. (1995), Global net primary production: combining ecology and remote sensing. *Remote Sens. Environ.* 51:74–88.

Floret, C., Pontanier, R., and Rambal, S. (1982), Measurement and modelling of primary production and water use in a south Tunisian steppe. *J. Arid Environ.* 5:77–90.

Gallo, K. P., Daughtry, C. S. T., and Bauer, M. E. (1985), Spectral estimation of absorbed photosynthetically active radiation in corn canopies. *Remote Sens. Environ.* 17:221–232.

Gamon, J. A., and Qiu, H. L. (1999), Ecological applications of remote sensing at multiple spatial scales. In: *Handbook of Functional Plant Ecology* (F. I. Pugnaire and F. Valladares, Eds.), Marcel Decker, New York, pp. 805–846.

Gamon, J. A., Field, C. B., Goulden, M. L., Griffin, K. L., Hartley, A. E., Joel, G., Penuelas, J., and Valentini, R. (1995), Relationships between NDVI, canopy structure, and photosynthesis in three Californian vegetation types. *Ecol. Appl.* 5:28–41.

Gao, B. C., and Goetz, A. F. H. (1995), Retrival of equivalent liquid water thickness and information related to biochemical components of vegetation canopies from AVIRIS data. *Remote Sens. Environ.* 52:155–162.

Goward S. N., Tucker, C. J., and Dye, D. G. (1985), North American vegetation patterns observed with the NOAA-7 advanced very high resolution radiometer. *Vegetatio* 64: 3–14.

Green, C. F. (1987), Nitrogen nutrition and wheat growth in relation to absorbed solar radiation. *Agric. For. Meteorol.* 41:207–248.

Green, R. O., Conel, J. E., and Roberts, D. A. (1995), Measurements of atmospheric water vapor, leaf liquid water and reflectance with AVIRIS in the Boreal-Ecosystem-Atmosphere Study: initial results. In *AVIRIS Imagery: Summaries of the 5th Annual Jet Propulsion Laboratory's Airbone Earth Science Workshop*, Vol. 1 (R.O. Green, Ed.), Jet Propulsion Laboratory, Pasadena, CA, pp. 95–98.

Hanan, N. P., Prince, S. D., and Bégué, A. (1995), Estimation of absorbed photosynthetically active radiation and vegetation net production efficiency using satellite data. *Agric. For. Meteorol.* 76:259–276.

Hill, M. J., Donald, G. E., and Vickery P. J. (1999), Relating radar backscatter to biophysical properties of temperate perennial grassland. *Remote Sens. Environ.* 67:15–31.

Jackson, R. D., Reginato, R. J., and Idso, S. B. (1977), Wheat canopy temperature: a practical tool for evaluating water requirements. *Water Resour. Res.* 13:651–656.

Körner, C. (1991), Some often overlooked plant characteristics as determinants of plant growth: a reconsideration. *Funct. Ecol.* 5:162–173.

Kumar, M., and Monteith, J. L. (1982), Remote sensing of crop growth. In *Plants and the Daylight Spectrum* (H. Smith, Ed.), Academic Press, London, pp. 133–144.

Lauenroth, W. K., Hunt, H. W., Swift, D. M., and Singh, J. S. (1986), Estimating aboveground net primary production in grasslands: a simulation approach. *Ecol. Model.* 33:297–314.

Law, B. E., and Waring, R. H. (1994), Remote sensing of leaf area index and radiation intercepted by understory vegetation. *Ecol. Appl.* 4:272–279.

Leblon, B., Guerif, M., and Baret, F. (1991), The use of remotely sensed data in estimation of PAR use efficiency and biomass production of flooded rice. *Remote Sens. Environ.* 38:147–158.

Le Houérou H. N., and Hoste, C. H. (1977), Rangeland production and annual rainfall relations in the Mediterranean basin and in the African Sahelo-Sudanese zone. *J. Range Manag.* 30:180–198.

Le Houérou, H. N. (1984), Rain use efficiency: a unifying concept in arid-land ecology. *J. Arid Environ.* 7:213–247.

Le Roux, X., Gauthier, H., Bégué, A., and Sinoquet, H. (1997), Radiation absorption and use by humid savanna grassland:

assessment using remote sensing and modelling. Agric. For. Meteorol. 85:117–132.

Long, S. P., Garcia Moya, E., Imbamba, S. K., Kamnalrut, A., Piedade, M. T. F., Scurlock, J. M. O., Shen, Y. K., and Hall, D. O. (1989), Primary productivity of natural grass ecosystems of the tropics: a reappraisal. *Plant Soil* 115:155–166.

Monteith, J. L. (1972), Solar radiation and productivity in tropical ecosystems. *J. Appl. Ecol.* 9:747–766.

Moran, M. S., and Jackson, R. D. (1991), Assessing the spatial distribution of evapotranspiration using remotely-sensed inputs. *J. Environ. Qual.* 20:725–737.

Moran, M. S., Rahman, A. F., Washburne, J. C., Goodrich, D. C., Weltz, M. A., and Kustas, W. P. (1996), Combining the Penman-Monteith equation with measurements of surface temperature and reflectance to map regional evaporation rates. *Agric. For. Meteorol.* 80:87–109.

Mougin, E., Lo Seen, D., Rambal S., Gaston, A., and Hiernaux, P. (1995), A regional Sahelian grassland model to be coupled with multispectral satellite data: I. Model description and validation. *Remote Sens. Environ.* 52:181–193.

Myneni, R. B., and Williams, D. L. (1994), On the relationship between FAPAR and NDVI. *Remote Sens. Environ.* 49: 200–211.

Nouvellon, Y., Rambal, S., Lo Seen, D., Moran, M. S., L'homme, J. P., Bégué, A., Chehbouni, A. G., and Kerr, Y. (1999), Modelling of daily fluxes of water and carbon from semiarid grasses. *Agric. For. Meteorol.* (in press).

Osborn, H. B., Lane, L. J., and Hundley, J. F. (1972), Optimum gaging of thunderstorm rainfall in Southeastern Arizona. *Water Resour. Res.* 8:259–265.

Paruelo, J. M., Epstein, H. E., Lauenroth, W. K., and Burke, I. C. (1997), ANPP estimates from NDVI for the central grassland region of the United States. *Ecology* 78:953–958.

Peñuelas, J., Filella, I., Biel, C., Serrano, L., and Savé, R. (1993), The reflectance at the 950–970 nm region as an indicator of plant water status. *Int. J. Remote Sens.* 14: 1887–1905.

Peñuelas, J., Piñol, J., Ogaya, R., and Filella, I. (1997), Estimation of plant water concentration by the reflectance water index WI (R970/R900). *Int. J. Remote Sens.* 18:2863–2868.

Pinter, P. J., Jackson, R. D., Idso, S. B., and Reginato, R. J. (1983), Diurnal patterns of wheat spectral reflectances. *IEEE Trans. Geosci. Remote Sens.* 21:156–163.

Pinter, P. J., Jackson, R. D., Ezra, C. E., and Gausman, H. W. (1985), Sun angle and canopy architecture effects on the reflectance of six wheat cultivars. *Int. J. Remote Sens.* 6: 1813–1825.

Potter, C. S., Randerson, J. T., Field, C. B., Matson, P. A., Vitousek, P. M., Mooney, H. A., and Klooster, S. A. (1993), Terrestrial ecosystem production: a process model based on global satellite and surface data. *Global Biogeochem. Cycles* 7:811–841.

Prince, S. D. (1991a), Satellite remote sensing of primary production: comparison of results for Sahelian grasslands 1981–1988. *Int. J. Remote Sens.*, 12:1301–1312.

Prince, S. D. (1991b), A model for regional primary production for use with coarse resolution satellite data. *Int. J. Remote Sens.* 12:1313–1330.

Prince, S. D., and Goward, S. N. (1995), Global primary production: a remote sensing approach. *J. Biogeogr.* 22: 815–835.

Rambal, S., and Cornet, A. (1982), Simulation de l'utilisation de l'eau et de la production végétale d'une phytocénose Sahélienne du Sénégal. *Acta Oecol. Oecol. Plant.* 4:381–397.

Roberts, D. A., Green, R. O., and Adams, J. B. (1997), Temporal and spatial patterns in vegetation and atmospheric properties from AVIRIS. *Remote Sens. Environ.* 62:223–240.

Ruimy, A. (1995), Modélisation de la productivité primaire nette continentale. Ph.D. thesis, Université Paris Sud.

Ruimy, A., Saugier, B., and Dedieu, G. (1994), Methodology for the estimation of terrestrial net primary production from remotely sensed data. *J. Geophys. Res.* 99:5263–5283.

Ruimy, A., Dedieu, G., and Saugier, B. (1996), TURC—terrestrial uptake and release of carbon by vegetation: a diagnostic model of continental gross primary productivity and net primary productivity. *Global Biogeochem. Cycles* 10: 269–285.

Running, S. W., and Hunt, E. R. (1992), Generalisation of a forest ecosytem process model for other biomes, Biome-BGC, and an application for global-scale models. In *Scaling Processes between Leaf and Landscale Level* (J. R. Ehleringer and C. Field, Eds.), Academic Press, San Diego, 388 p.

Runyon, J., Waring, R. H., Goward, S. N., and Welles, J. M. (1994), Environmental limits on net primary production and light-use efficiency across the Oregon transect. *Ecol. Appl.* 4:226–237.

Ryle, G. J. A. (1970), Partition of assimilates in an annual and a perennial grass. *J. Appl. Ecol.* 7:217–227.

Schmullius, C., and Furrer, R. (1992), Frequency dependence of radar backscattering under different moisture conditions of vegetation-covered soil. *Int. J. Remote Sens.* 12: 2233–2245.

Seguin, B., and Itier, B. (1983), Using midday surface temperature to estimate daily evaporation from satellite thermal IR data. *Int. J. Remote Sens.* 4:371–383.

Seguin, B., Assad, E., Freteaud, J. P., Imbernon, J., Kerr, Y., and Lagouarde, J. P. P. (1989), Use of meteorological satellites for water balance monitoring in Sahelian regions. *Int. J. Remote Sens.* 10:1101–1117.

Sellers, P. J. (1987), Canopy reflectance, photosynthesis, and transpiration: II. The role of biophysics in the linearity of their interdependence. *Remote Sens. Environ.* 21:143–183.

Sellers, P. J., Berry, J. A., Collatz, G. J., Field, C. B., and Hall, F. G. (1992), Canopy reflectance, photosynthesis and transpiration: III. A reanalysis using improved leaf models and a new integration scheme. *Remote Sens. Environ.* 42:187–216.

Singh, J. S., Lauenroth, W. K., and Steinhorst, R. K. (1975), Review and assessment of various techniques for estimating net aerial primary production in grasslands from harvest data. Bot. Rev. 41:181–232.

Steinmetz, S., Guerif, M., Delecolle, R., and Baret, F. (1990), Spectral estimates of the absorbed photosynthetically active radiation and light-use efficiency of a winter wheat crop subjected to nitrogen and water deficiencies. Int. J. Remote Sens. 10:1797–1808.

Tucker, C. J., Holben, B. N., Elgin, J. H., and McMurtrey, J. E. (1981), Remote sensing of total dry matter accumulation in winter wheat. *Remote Sens. Environ.* 11:171–190.

Tucker, C. J., Vanpraet, C. L., Sharman, M. J., and Van Ittersum, G. (1985), Satellite remote sensing of total herbaceous biomass production in the Senegalese Sahel: 1980–1984. *Remote Sens. Environ.* 17:233–249.

Ustin, S. L., Roberts, D. A., Pinzón, J., Jacquemoud, S., Gardner, M., Scheer, G., Castañeda, C. M., and Palacios-Orueta, A. (1998), Estimating canopy water content of chaparral shrubs using optical methods. *Remote Sens. Environ.* 65: 280–291.

Varlet-Grancher, C., Bonhomme, R., Chartier, M., and Artis, P. (1982), Efficience de la conversion de l'énergie solaire par un couvert végétal. *Acta Oecol. Oecol. Plant.* 3:3–26.

Weltz, M. A., Ritchie, J. C., and Fox, H. D. (1994), Comparison of laser and field measurements of vegetation height and canopy cover. *Water Resour. Res.* 30:1311–1319.

Wylie, B. K., Harrington, J. A., Jr., Prince, S. D., and Denda, I. (1991), Satellite and ground-based pasture production assessment in Niger: 1986–1988. *Int. J. Remote Sens.* 12: 1281–1299.