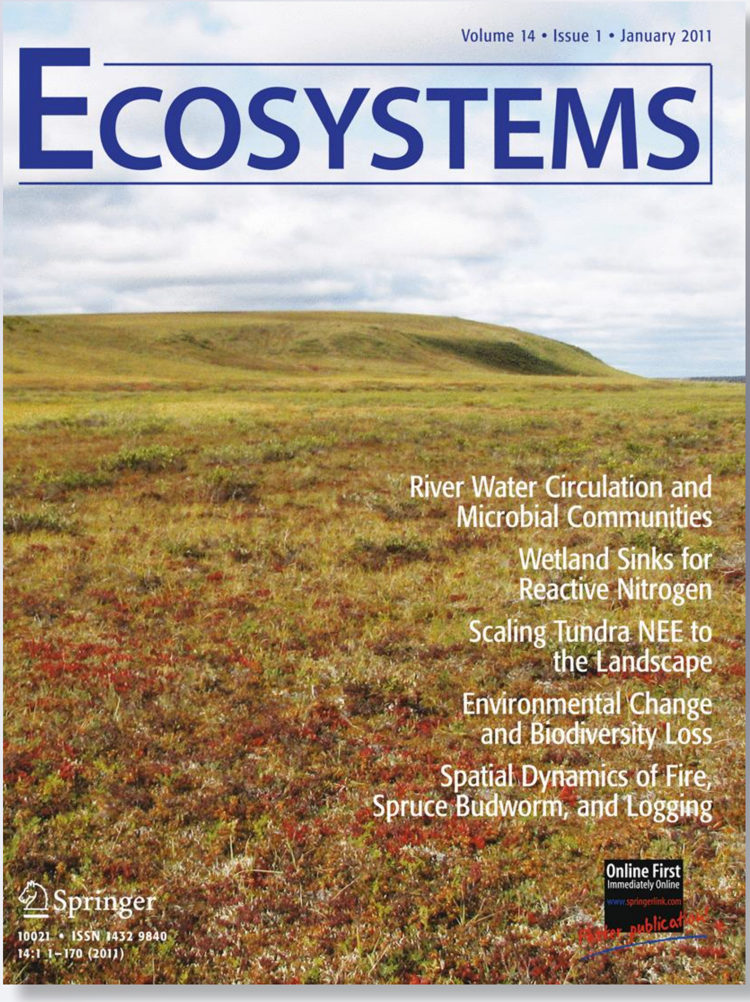
Variability in Light-Use Efficiency for Gross Primary Productivity on Great Plains Grasslands

Ecosystems

ISSN 1432-9840
Volume 14
Number 1

Ecosystems (2010) 14:15-27
DOI 10.1007/
s10021-010-9389-3



Ecosystems (2011) 14: 15–27
DOI: 10.1007/s10021-010-9389-3

ECOSYSTEMS

Variability in Light-Use Efficiency for Gross Primary Productivity on Great Plains Grasslands

H. Wayne Polley,[1]* Rebecca L. Phillips,[2] Albert B. Frank,[2]
James A. Bradford,[3] Phillip L. Sims,[3] Jack A. Morgan,[4] and James R. Kiniry[1]

[1]Grassland, Soil and Water Research Laboratory, USDA-Agricultural Research Service (ARS), 808 East Blackland Road, Temple, Texas 76502, USA; [2]Northern Great Plains Research Laboratory, USDA-ARS, Mandan, North Dakota 58554, USA; [3]Southern Plains Range Research Station, USDA-ARS, Woodward, Oklahoma 73801, USA; [4]Crops Research Laboratory, USDA-ARS, Ft. Collins, Colorado 80526, USA

ABSTRACT

Gross primary productivity (GPP) often is estimated at regional and global scales by multiplying the amount of photosynthetically active radiation (PAR) absorbed by the plant canopy (PARa) by light-use efficiency (ϵ_g; GPP/PARa). Mass flux techniques are being used to calculate ϵ_g. Flux-based estimates of ϵ_g depend partly on how PAR absorption by plants is modeled as a function of leaf area index (LAI). We used CO_2 flux measurements from three native grasslands in the Great Plains of USA to determine how varying the value of the radiation extinction coefficient (k) that is used to calculate PARa from LAI affected variability in estimates of ϵ_g for each week. The slope of linear GPP–PARa regression, an index of ϵ_g, differed significantly among the 18 site-years of data, indicating that inter-annual differences in ϵ_g contributed to the overall variability in ϵ_g values. GPP–PARa slopes differed among years and sites regardless of whether k was assigned a fixed value or varied as an exponential function of LAI. Permitting k to change with LAI reduced overall variability in ϵ_g, reduced the slope of a negative linear regression between seasonal means of ϵ_g and potential evapotranspiration (PET), and clarified the contribution of inter-annual differences in precipitation to variation in ϵ_g. Our results imply that greater attention be given to defining dynamics of the k coefficient for ecosystems with low LAI and that PET and precipitation be used to constrain the ϵ_g values employed in light-use efficiency algorithms to calculate GPP for Great Plains grasslands.

Key words: absorbed photosynthetically active radiation; CO_2 flux measurements; grassland; leaf area index; mixed grass prairie; precipitation; radiation extinction coefficient; shortgrass steppe.

INTRODUCTION

Gross primary productivity (GPP) is a key component of the carbon (C) cycle that must be determined to measure spatial patterns in C fluxes and understand inter-annual variability in C cycling. Ecosystem GPP often is calculated using algorithms that employ the light-use efficiency (LUE) concept (Running and others 2004; Yuan and others 2007).

Received 5 March 2010; accepted 20 September 2010;
published online 6 November 2010

Author Contributions: WP conceived study, analyzed data, and wrote the article. RP, AF, JB, PS, and JM performed research. JK contributed new methods and analyzed data.

Corresponding author; e-mail: wayne.polley@ars.usda.gov

With this method, GPP is derived by multiplying the amount of photosynthetically active radiation (PAR) that is absorbed by the plant canopy (PARa) by a conversion or LUE (ϵ_g), the ratio of GPP to PARa.

Remote sensing methods have been developed to determine the fraction of PAR that is absorbed by the canopy and, ultimately, PARa (for example, Gower and others 1999). Methods to remotely estimate LUE are under development (Drolet and others 2008), but ϵ_g usually is assigned either a constant value (Veroustraete and others 2002) or is calculated by multiplying a potential value by modifiers meant to represent effects of environmental stressors (Running and others 2004; Schwalm and others 2006). Environmental modifiers may take several forms, but usually are calculated using near real-time environmental conditions. A similar method of accounting for environmental effects on C fluxes is used in models in which GPP is calculated using PAR alone (Gilmanov and others 2005).

Eddy covariance and other mass flux techniques are being used to refine estimates of ϵ_g for LUE algorithms and to quantify environmental effects on ϵ_g (Schwalm and others 2006; Yuan and others 2007). The ϵ_g is calculated by dividing GPP derived from daily measurements of C fluxes by the PARa, the product of incident PAR and the fraction of PAR absorbed by the plant canopy (f_{PARa}). The f_{PARa}, in turn, often is calculated as a function of leaf area index (LAI) and a radiation extinction coefficient, k, using the Beer–Lambert Law. This approach of calculating PARa also is used in many canopy photosynthesis models (Ruimy and others 1999). The radiation extinction coefficient usually is assigned a fixed value, although most researchers acknowledge that k varies seasonally and inter-annually with changes in leaf angle and age, canopy height, LAI, and other factors (Tahiri and others 2006; Irmak and Mutiibwa 2008). Because the extinction coefficient commonly is determined at midday when canopies are fully developed, the practice of using a fixed value of k to calculate f_{PARa} and PARa may be problematic for grassland ecosystems on which LAI often is small and varies widely among years in response to inter-annual variation in precipitation (Nouvellon and others 2000a; Flanagan and others 2002; Frank 2002; Xu and Baldocchi 2004). Indeed, even the PARa of canopies of monocultures may be underestimated at low LAI when calculated using a fixed k value (Tahiri and others 2006; Irmak and Mutiibwa 2008), leading to an overestimation of ϵ_g at low LAI, a negative correlation between ϵ_g and LAI, and greater variation in ϵ_g than would result if k was varied to accommodate seasonal and inter-annual change in canopy properties.

Environmental "stresses," such as extreme temperatures or water shortages, are assumed to reduce ϵ_g below its potential value. Environmental effects on ϵ_g commonly are modeled using near real-time environmental conditions to derive a scalar or other multiplier of potential ϵ_g. This approach of using short-term (days, weeks) changes in the environment to describe variation in ϵ_g is most effective if a given change in the environment has the same effect on ϵ_g among years and sites. Effects of the environment on ϵ_g may differ among years if inter-annual dynamics of GPP and ϵ_g are determined more by differences in weather patterns expressed over months and years than by brief changes in the environment. The assumption that environmental effects on C fluxes are invariant has proven problematic in accounting for inter-annual variability in net ecosystem exchange on rangelands (Polley and others 2010a) and other ecosystems (Hui and others 2003). Flux responses to environmental change differed among years because of inter-annual variation in biological factors that regulate C exchange (Polley and others 2010b).

We used measurements of CO_2 fluxes from three grasslands in the Great Plains of USA to determine how using a variable as opposed to fixed value of the radiation extinction coefficient, k, to calculate PARa affected (1) the contribution of inter-annual variation to total variance in ϵ_g among grasslands and years and (2) correlations between inter-annual differences in ϵ_g and among-year variation in precipitation and potential evapotranspiration (PET) summed over periods of months. We predicted that (1) ϵ_g, as reflected in the slope of a linear relationship between GPP and PARa, would vary significantly among years on these grasslands, (2) allowing k to vary as a function of LAI would reduce the contribution of inter-annual differences in ϵ_g to total variation among ϵ_g estimates, and (3) allowing k to vary as a function of LAI would strengthen correlations between seasonal means of ϵ_g and both precipitation and PET. By varying k, we expected to reduce any correlation between ϵ_g and LAI and thereby strengthen relationships between ϵ_g and both precipitation and PET.

METHODS

Study Sites

We measured CO_2 exchange on three native grassland ecosystems in the Great Plains Region of

USA: northern mixed-grass prairie at Mandan, North Dakota, shortgrass steppe at Nunn, Colorado, and southern mixed-grass prairie at Woodward, Oklahoma (Table 1). Dominant plant species at Mandan include the C_4 perennial grasses *Bouteloua gracilis* [H.B.K.] Lag. Ex Griffiths (blue grama), *Schizachyrium scoparium* [Michx.] Nash (little bluestem), and *Bouteloua curtipendula* [Michx.] Torr. (side-oats grama) and C_3 grasses *Hesperostipa comata* Trin. and Rupr. (needle-and-thread) and *Poa pratensis* L. (Kentucky bluegrass) (Frank and others 2001). The C_4 perennial grasses *B. gracilis* and *Buchloe dactyloides* (Nutt) [buffalograss] dominate the shortgrass steppe, but several C_3 grasses [for example, *Pascopyrum smithii* (Rydb.) Love (western wheatgrass) and *H. comata*], forbs, and small shrubs also occur. Vegetation on southern mixed-grass prairie includes several C_4 grasses, including the tallgrasses *S. scoparium* and *Andropogon gerardii* var. *paucipilus* (Nash) Fern (sand bluestem), mid-grass *Sporobolus cryptandrus* (Torr.) Gray (sand dropseed), and short grasses *B. gracilis* and *B. dactyloides*. The major C_3 species present are the grass *Poa arachnifera* Torr. (Texas bluegrass) and perennial forb *Ambrosia psilostachya* Torr. (sand sagebrush) (Frank and others 2001). Grasslands were considered to be in good ecological condition based on species composition and were not grazed by livestock, burned, or fertilized during the period of measurements because of the difficultly of uniformly applying these treatments across grasslands. Prior to measurements, these grasslands had either not been grazed for 10 or more years or had been lightly to moderately grazed by livestock. Svejcar and others (2008) provide a description of soils and land-use history for each ecosystem.

CO_2 Fluxes and Environmental Variables

GPP was calculated using measurements of net ecosystem exchange of CO_2 (NEE) with Bowen ratio/energy balance (BREB) instrumentation (Model 023/CO_2 Bowen ratio system, Campbell Scientific, Inc., Logan, Utah, USA) as detailed by Polley and others (2010a). Carbon dioxide fluxes were calculated by multiplying turbulent diffusivity by the change in the density of CO_2 measured between 1 and 2 m above the canopy and correcting for differences in water vapor density (Webb and others 1980). When turbulent diffusivity estimated by the BREB approach failed, as evidenced by differences in signs of the sensible/latent heat flux calculations and the temperature/water vapor gradient, we calculated turbulent diffusivity using wind speed, atmospheric stability, and canopy height (Dugas and others 1999). This alternative method of estimating diffusivity was used in about 10% of calculations, mostly at night. Frank and others (2001) showed that CO_2 fluxes measured at night on grassland using the BREB method were only slightly smaller than the sum of estimated night-time plant and soil respiratory losses. Fluxes calculated using the BREB method have been shown to be similar to those estimated from biomass production (Dugas and others 1999), canopy chambers (Angell and others 2001), and the eddy covariance technique (Wolf and others 2008). We did not attempt to gap-fill missing data, which accounted for less than 1% of data points during daylight hours and 2% of data points at night (Svejcar and others 2008). Latent heat was determined as the energy remaining after subtracting soil heat flux and sensible heat flux from net radiation. Actual evapotranspiration (AET) was calculated by dividing the latent heat of evaporation by the latent heat of vaporization. Flux toward the surface was considered to be positive in sign.

Svejcar and others (2008) describe measurements of additional environmental variables, including soil temperature (T_s), wind speed (WS), relative humidity (RH), vapor pressure (e), net radiation (R_n), and air temperature (T_a). Photosynthetically active radiation was calculated by multiplying R_n ($W\ m^{-2} = J\ m^{-2}\ s^{-1}$) by 3.0 ($\mu mol\ W^{-1}\ s^{-1}$), as determined from year-long measurements of PAR and Rn at a companion flux site (Polley and others 2010a). Net radiation is the difference between solar

Table 1. Location, Vegetation Type, Site Characteristics, and the Years and the Interval Considered in Each Growing Season for Flux Measurements for Grassland Ecosystems in this Study

Location	Vegetation type	Mean annual precipitation (mm)	Latitude (°N)/ longitude (°W)	Years	Max./min. precip. (mm)	Interval (day)
Mandan, North Dakota (ND)	Northern mixed-grass prairie	482	46°46′/100°55′	1995–2001	643/325	113–287
Nunn, Colorado (CO)	Shortgrass steppe	321	40°41′/104°45′	1998–2001	420/233	127–294
Woodward, Oklahoma (OK)	Southern mixed-grass prairie	728	36°36′/99°35′	1999–2005	802/454	120–252

radiation and reflectivity plus re-radiation and therefore includes components of the energy budget, including convective heating of air and the heating of soil, that are not relevant for PAR. Nevertheless, daytime means of PAR and R_n were strongly and linearly correlated ($r^2 = 0.85$, $n = 893$). Following Stephenson (1990), we define the parameter ''evaporative deficit'' as evaporative demand not met by available water. A value of evaporative deficit for each day was calculated as the difference between daily values of PET and AET. PET was calculated with the Penman–Monteith equation using measurements of R_n, WS, T_a, and e. To reduce fluctuations inherent in daily values, we divided each day into 20-min periods, then calculated weekly averages of NEE, PAR, and T_s for each 20-min period (20-min means). Averages of NEE and PAR from each 20-min period during the day were summed to provide a mean daily value of each variable for each week. For each week during each growing season, we also calculated daily averages of T_a and other environmental variables. We determined the weekly sum of precipitation (ppt1) and the mean of precipitation per week for the current week and the previous 1–7 weeks (denoted as ppt2–ppt8).

GPP

Ecosystem GPP (g C m^{-2} day^{-1}) was calculated by subtracting ecosystem respiration during daylight from NEE. R_e was estimated for each 20-min period during daylight (PAR > 20 µmol m^{-2} s^{-1}) as:

$$R_e = R_{10} Q_{10}^{((T_s - 10)/10)} \qquad (1)$$

where T_s is soil temperature, R_{10} is ecosystem respiration rate at 10°C, and Q_{10} is the temperature sensitivity of R_e for a 10°C change in T_s. R_{10} and Q_{10} were calculated for each week by fitting a nonlinear, least squares regression model (Gauss–Newton Method) to 20-min means of respiration (=NEE) and T_s at night. Estimates of the apparent temperature sensitivity of respiration (Q_{10}) may be confounded if photosynthetic activity and soil water content covary with temperature, as often occurs during periods of several days (Davidson and others 2006; Polley and others 2006). To reduce the influence of these confounding variables on Q_{10}, we calculated a mean value of Q_{10} for each year following methods of Reichstein and others (2005). For each site and year, we fit equation (1) to 20-min data from 3-week periods created by shifting the initial week of the period by 1 week before each regression was fit. A value of Q_{10} for each season at each site then was derived by averaging the Q_{10} values estimated for each 3-week period using the inverse of the standard error of estimate as the weighting factor. We set the Q_{10} parameter in equation (1) to this average value for the growing season, then re-fit the respiration model to derive R_{10} for each week. A daily average of GPP and R_e for each week was calculated by summing 20-min estimates during the daylight period.

PARa and ϵ_g

Ecosystem GPP is correlated with the amount of PAR that is absorbed by the plant canopy (PARa; MJ m^{-2}) where

$$\text{GPP} = \text{PARa} \times \varepsilon_g = \text{PAR} \times f_{\text{PARa}} \times \varepsilon_g \qquad (2)$$

and ϵ_g is ecosystem LUE (g C MJ^{-1} PARa).

A daily average of PARa for each week was calculated by summing weekly averages of incident PAR for each 20-min period over the daylight period by an estimate of the fraction of PAR absorbed by the plant canopy (f_{PARa}). The f_{PARa} was calculated from seasonal trajectories in LAI using the Beer–Lambert Law:

$$f_{\text{PARa}} = \left(1 - e^{(-k \times \text{LAI})}\right) 0.95, \qquad (3)$$

where k is the radiation extinction coefficient and 0.95 is the proportion of intercepted PAR that is absorbed by plants (Schwalm and others 2006). A value of ϵ_g for each week was determined by dividing the sum of weekly averages of GPP for each 20-min period during the daylight period (the daily average of GPP) by the sum of weekly averages of PARa for each 20-min period.

Two approaches were used to derive the extinction coefficient. First, k was assigned a fixed value appropriate for each site (fixed k). We calculated that $k = 0.5$ for mixed-grass prairie at Mandan using data on PAR measured above and below the plant canopy with quantum sensors (R. Phillips, unpublished data). We used a value of $k = 0.6$ for shortgrass steppe, as reported by Nouvellon and others (2000a), and of $k = 0.4$ for southern mixed-grass prairie (Kiniry and others 2007). Second, k was modelled as a function of LAI for all sites (variable k). Several factors may contribute to differences in k as LAI varies within and among grasslands. Included are differences in the relative contributions of species with different leaf angles to the plant canopy, seasonal change in the horizontal and vertical distributions of leaves (Nouvellon and others 2000a), and within-species shifts from more horizontal to vertical leaves as plants develop (Tahiri and others 2006). To estimate effects of LAI on k, we first calculated a k value for each week in the full data set using measured values of GPP, PAR, and LAI for each week and the average value of ϵ_g calculated using data from all sites and years combined ($\epsilon_g = 1.76$ g C MJ^{-1} as described below; equations 2 and 3). A regression equation was fit to the relationship between calculated values of *k* and LAI. Values of PARa and ϵ_g for each week and grassland then were recalculated by allowing *k* to vary as a function of LAI. This procedure partitions the variation in GPP–PARa relationships between ϵ_g and the *k* parameter.

Leaf area was measured at four positions surrounding Bowen ratio equipment on each of the three grasslands at approximately 3-week intervals (Mandan, 7–11 measurements per season) or 4-week intervals during each growing season (Nunn, 6–7 measurements per season; Woodward, 5 measurements per season). On each sampling date, one quadrat (0.25 m^2) was randomly placed within each of four permanently located plots (each 30 m × 30 m) on each grassland. Vegetation in each quadrat was clipped to ground level, and the surface area of green tissues (leaf area) was measured with a photoelectric meter. Daily values of leaf area per unit of soil area, LAI, were obtained by linearly interpolating LAI between measurement dates. Estimates of LAI at the mid-point of each week for which GPP was calculated were used to calculate f_{PARa}.

Statistics

We considered data collected during the growing season period when LAI was measured on each grassland (Table 1). Linear regression functions were fit to relationships between daily averages of GPP and PARa for each week and between seasonal means of GPP and both average LAI and annual precipitation. Linear regression analysis also was used to determine the contribution of the among-week change in environmental variables (for example, T_a, evaporative deficit, and time-lagged indices of precipitation) that was not accounted for by change in LAI to variability in estimates of ϵ_g for each week. We used a homogeneity-of-slopes (HOS) regression model (Hui and others 2003) to determine the contribution of inter-annual differences in slopes of GPP–PARa regressions to variance in GPP–PARa relationships.

RESULTS

Seasonal Means of GPP

Means of daily averages of C fluxes varied widely among years. GPP differed by greater than a factor of two among years at Mandan and Nunn and by a similar absolute, albeit smaller relative, amount at Woodward (Figure 1). Averaged for all years of record, growing season means of daily values of GPP and NEE were greatest for mixed-grass prairie at Woodward (4.9 and 2.6 g C m^{-2} day^{-1}, respectively) and similar for short-grass steppe at Nunn and mixed prairie at Mandan (2.9 and 1.8 g C m^{-2} day^{-1}, respectively). By contrast, the ratio of R_e to GPP was similar among years at a given site and was similar among sites. The R_e/GPP averaged 0.41, 0.37, and 0.47 at Mandan, Nunn, and Woodward, respectively.

Variation in GPP among years and sites was linked to variation in precipitation. Growing season averages of GPP increased linearly as annual precipitation increased when data from all years and sites were considered (Figure 2). GPP increased as precipitation increased partly because average values of LAI, and by inference, of PARa also increased with greater precipitation. As a result, average GPP was a positive linear function of seasonal means of LAI when data from all years and sites were considered [GPP (g C m^{-2} day^{-1} = 2.04 + 3.15 × LAI, $r^2 = 0.85$, $P < 0.0001$, $n = 18$]. Correlations between precipitation and both GPP and LAI were not significant when assessed with data from individual sites ($P = 0.06$–0.37 for GPP; $P = 0.08$–0.29 for LAI).

GPP–PARa Relationships—Fixed *k*

The shape of the relationship between daily averages of GPP and PARa differed among sites when PARa was calculated assuming a fixed value of *k* for each grassland (Figure 3). Daily averages of GPP

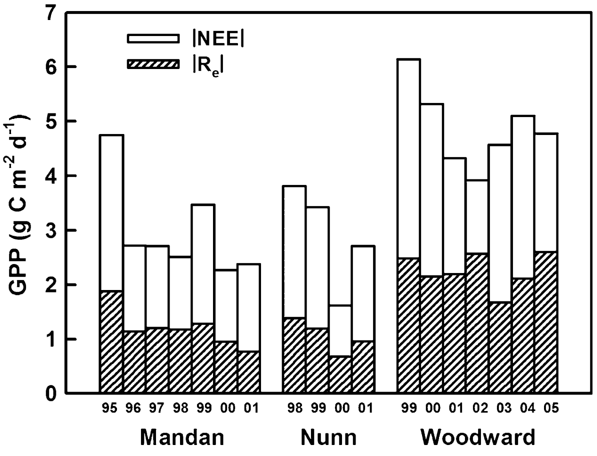


Figure 1. The contribution of net ecosystem exchange (NEE) and ecosystem respiration (R_e) to mean values of daily GPP for each growing season and grassland.

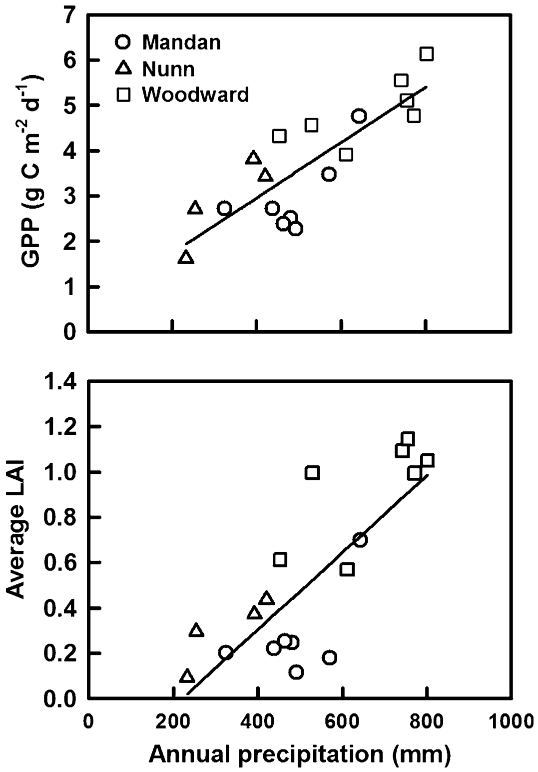


Figure 2. Relationships between growing season means of GPP per day (*upper panel*) or the average value of LAI per season (*lower panel*) and annual precipitation (ppt). Data from all years and grasslands combined (n = 18) were fit with linear functions (GPP = 0.518 + 0.006 × ppt, $r^2 = 0.68$, $P < 0.0001$; LAI = −0.376 + 0.002 × ppt, $r^2 = 0.63$, $P < 0.0001$).

and PARa were calculated for each week by summing weekly means of measurements from each 20-min period during daylight. The daily average of GPP from each week was a linear function of daily averages of PARa at Nunn and Woodward for all years of data combined. The GPP–PARa relationship was best fit by a rectangular hyperbola at Mandan. The non-linear relationship between GPP and PARa at Mandan resulted largely from strongly hyperbolic relationships in 2 of 7 years. GPP at Mandan approached maximum values of about 3.5 g C m^{-2} day^{-1} when PARa reached 1.0 and 1.5 MJ m^{-2} day^{-1} in 2000 and 2001, respectively (Figure 4). GPP for Mandan was a linear function of PARa when assessed using data collected in 1995 through 1999 and at PARa values less than 1.0 and 1.5 MJ m^{-} day^{-1} in 2000 and 2001, respectively.

Low autumn and winter precipitation may have contributed to the hyperbolic response of GPP to PARa at Mandan in 2000 and 2001. Precipitation summed for November through February was low during the 2000 and 2001 growing seasons (61 and 51 mm, respectively) compared to that for most other years (range from 45 to 177 mm).

A simple linear regression on PARa explained 55% of the variance in GPP when assessed with data from all sites and years combined ($P < 0.0001$, $n = 364$). Excluding data from the non-linear part of GPP–PARa curves in 2000 and 2001 for Mandan (at PARa values >1.0 and 1.5 MJ m^{-2} day^{-1}, respectively), increased the r^2 of the regression model from 0.55 to 0.59, where GPP (g C m^{-2} day^{-1}) = 1.44 + 1.23 × PARa (MJ m^{-2} day^{-1}), $P < 0.0001$, $n = 340$. A regression through the origin had a slope of 1.76 when data from all sites were considered ($n = 340$), implying an average ϵ_g of 1.76 g C MJ^{-1} for these 18 site-years of data.

Slopes of GPP–PARa relationships differed significantly among years when PARa was calculated using a fixed k value, indicating that inter-annual differences in LUE contributed significantly to the overall variability in weekly estimates of ϵ_g (Tables 2, 3). Allowing for inter-annual differences in GPP–PARa slopes increased the r^2 of the GPP–PARa regression model from 0.59 to 0.74. Means of ϵ_g values varied among years from 2.3 to 4.5 g C MJ^{-1} at Mandan, 1.7 to 3.9 g C MJ^{-1} at Nunn, and 1.4 to 2.2 g C MJ^{-1} at Woodward.

Regulation of ϵ_g Calculated with a Fixed k

Among-week changes in environmental variables explained little of the variation in ϵ_g not accounted for by changes in LAI. Estimates of ϵ_g for each week decreased exponentially as LAI increased when analyzed across data from all years and sites combined ($\epsilon_g = 1.52 + 3.49 \times e^{(-3.58\times\mathrm{LAI})}$, $r^2 = 0.44$, $P < 0.0001$, $n = 340$). The variation in T_a and ppt8 that was not accounted for by among-week changes in LAI was, at best, weakly correlated with variation in ϵ_g ($P = 0.81$ and $r^2 = 0.03$, $P = 0.002$, respectively).

Seasonal means of ϵ_g were negatively correlated with PET summed over the first 3 months of the growing season, May through July (Figure 5). The correlation between ϵ_g and PET (mm) was significant only for Nunn when assessed with data from individual sites, however ($\epsilon_g = 11.177 - 0.026 \times$ PET, $r^2 = 0.97$, $P = 0.009$, $n = 4$). Means of ϵ_g from each growing season declined exponentially as LAI increased (Figure 6).

GPP–PARa Relationships—Variable k

Over the range of LAI values encountered in these grasslands, fPARa and, at a given value of PAR, PARa are slightly curvilinear functions of LAI when

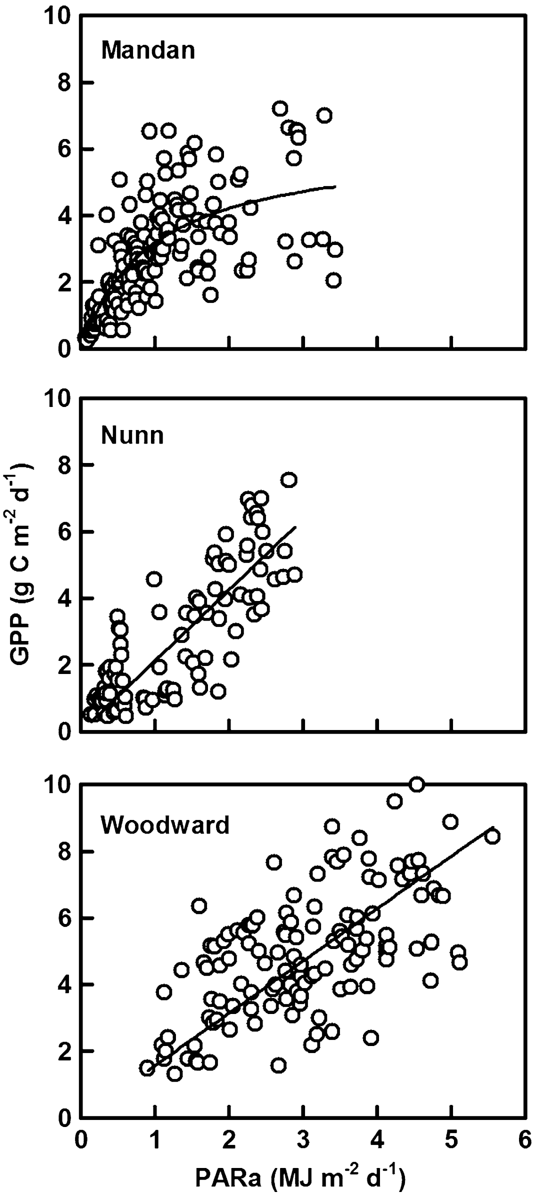


Figure 3. The relationship between GPP and PARa at each of three grassland sites. An average daily value of GPP and PARa was calculated for each week during each growing season at each site. Data from Mandan were fit with a rectangular hyperbola [GPP = ((6.23 × PARa)/(0.96 + PARa)), $r^2 = 0.51$, $P < 0.0001$, $n = 150$]. Data from Nunn and Woodward were fit with linear regressions through the origin with slopes of 2.12 ($n = 89$) and 1.57 ($n = 123$), respectively.

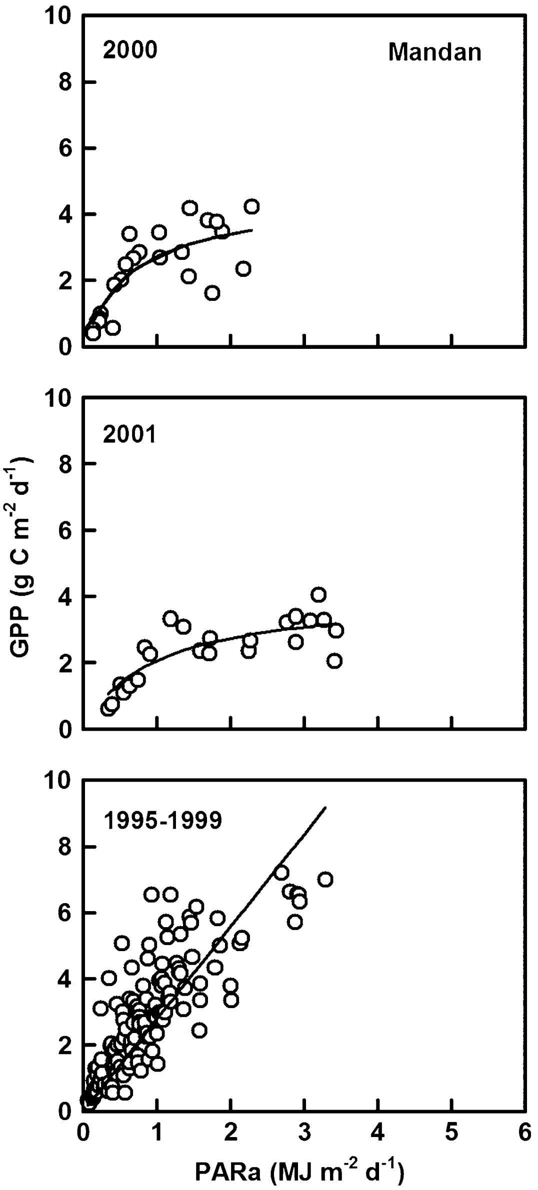


Figure 4. The relationship between GPP and PARa for the grassland at Mandan during each of three periods. An average daily value of GPP and PARa was calculated for each week during each growing season. Data from 2000 and 2001 were fit with a rectangular hyperbola [GPP = ((a × PARa)/(b + PARa))] where $a = 4.53$ and 4.08 and $b = 0.66$ and 0.98, respectively. Data from remaining years plus readings in 2000 and 2001 at <1.0 and 1.5 MJ m^{-2} d^{-1} PARa, respectively, were fit with a linear function through the origin (slope = 2.79, $n = 128$).

calculated with the fixed k values we used (0.4–0.6). The exponential relationship we observed between both weekly values and seasonal averages of ϵ_g and LAI (Figure 6) thus may have resulted partly because we underestimated PARa at low LAI by assigning k a fixed value, rather than because GPP was high relative to PARa when LAI was low. To assess effects of varying the value of k on ϵ_g, we first calculated a k value for each week in the full data set by assuming that ϵ_g remained constant at the average value determined from

Table 2. The Analysis of Variance of a Separate-Slopes Regression Model of the Relationship Between GPP and PARa for Three Grassland Ecosystems

Source	Df	SS	*F*	Proportion
Model (fixed *k*)	18	1114.98	50.44***	0.737
PARa	1	885.80	715.6***	0.586
PARa × year	17	229.18	10.9***	0.151
Error	321	397.35	–	–
Total	339	1512.33	–	
Model (variable *k*)	18	1108.87	49.01***	0.733
PARa	1	938.78	746.91***	0.621
PARa × year	17	170.09	7.96***	0.112
Error	321	430.46	–	
Total	339	1512.33	–	

The PARa was calculated by assuming that the radiation extinction coefficient (k) was either fixed (fixed k) or varied as an exponential function of LAI (variable k). Proportion is the portion of variance in GPP explained by variation in PARa alone (PARa), inter-annual variability in GPP–PARa slopes (PARa × year), and the full separate-slopes model (Model).
$^{***}P < 0.0001$.

Table 3. Slopes of Relationships Between Average Daily Averages of GPP (g C m^{-2} day^{-1}) and PARa (MJ m^{-2} day^{-1}) for Each Week

Source	Fixed *k*		Variable *k*	
	GPP–PARa slope	Standard error	GPP–PARa slope	Standard error
Mandan, North Dakota				
1995	2.12	0.14	2.73	0.16
1996	3.28	0.31	2.58	0.20
1997	3.15	0.29	2.49	0.18
1998	2.21	0.25	1.94*	0.17
1999	4.67	0.37	3.01	0.20
2000	3.43	0.75	2.57	0.36
2001	2.04*	0.46	1.90*	0.28
Nunn, Colorado				
1998	2.29	0.16	2.48	0.15
1999	1.76	0.14	2.14	0.16
2000	3.25	0.64	2.82	0.34
2001	1.74	0.17	2.06	0.16
Woodward, Oklahoma				
1999	1.75	0.11	2.19	0.17
2000	1.46*	0.11	1.87	0.12
2001	1.87	0.13	1.81*	0.12
2002	1.73	0.16	1.75*	0.13
2003	1.21*	0.11	1.64*	0.10
2004	1.31*	0.10	1.75*	0.12
2005	1.34*	0.09	1.69*	0.12

Slopes were derived for each year of measurements for each of three grassland ecosystems. The PARa was calculated using values of the radiation extinction coefficient (k) that were fixed at 0.5, 0.6, and 0.4 for Mandan, Nunn, and Woodward, respectively, (column headed ''fixed k'') or varied as an exponential function of LAI across all grasslands (column headed ''variable k'').
Slopes that are labeled with an asterisk (*) did not differ from the minimum slope listed in the column.

linear regression of GPP on PARa, 1.76 g C MJ^{-1}. The result was an exponential relationship between calculated values of *k* and LAI (Figure 7) that, as expected, was similar in shape to the relationship we observed between ϵ_g and LAI when *k* was assigned a fixed value. Calculated values of *k* were linearly correlated with the natural logarithm of LAI, ln(LAI), where $k = -0.37 \times \ln(\mathrm{LAI}) + 0.41$

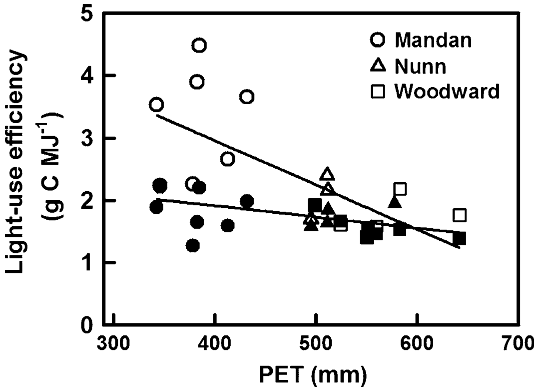


Figure 5. Relationships between growing season means of ecosystem LUE (ϵ_g) and PET summed for May through July each season for three grasslands. The value of the radiation extinction coefficient (k) used to calculate ϵ_g was either fixed for each grassland (*open symbols*) or varied as a common function of LAI for all grasslands (*closed symbols*). Means of ϵ_g declined linearly as PET increased [$\epsilon_g = 5.794 - 0.007 \times \text{PET}$, $r^2 = 0.44$, $P = 0.002$ (fixed k) and $\epsilon_g = 2.634 - 0.002 \times \text{PET}$, $r^2 = 0.38$, $P = 0.005$ (variable k)]. Both regressions were fit after excluding one outlying point ($n = 17$). One outlier is omitted from the figure for clarity [$\epsilon_g = 3.93$ g C MJ^{-1} (fixed k); PET = 578 mm].

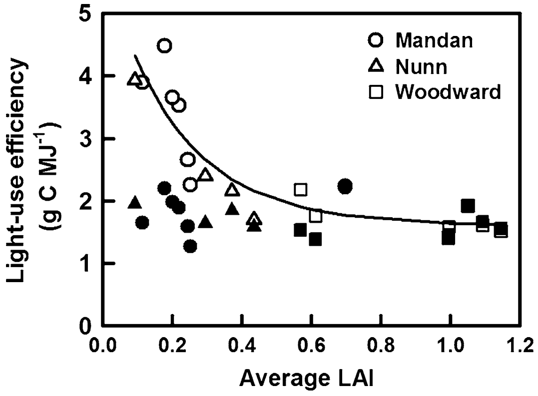


Figure 6. Relationships between growing season means of ecosystem LUE (ϵ_g) and seasonal means of LAI for three grasslands. The value of the radiation extinction coefficient (k) used to calculate ϵ_g was either fixed for each grassland (*open symbols*) or varied as a common function of LAI for all grasslands (*closed symbols*). Means of ϵ_g calculated with a fixed k declined exponentially as LAI increased ($\epsilon_g = 1.60 + 4.16 \times e^{(-4.63 \times \text{LAI})}$, $r^2 = 0.80$, $P < 0.0001$, $n = 18$). There was no correlation between ϵ_g calculated with a variable k and LAI ($P = 0.31$).

($r^2 = 0.48$, $P < 0.0001$, $n = 340$). The k increased from 0.32 to 0.63 and 1.28 as LAI declined from 1.5 to 0.5 and 0.1.

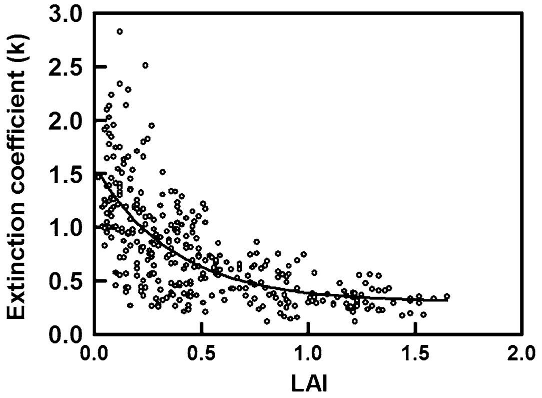


Figure 7. The relationship between estimates of the radiation extinction coefficient (k) for each week and LAI for three grasslands. The k parameter was calculated using measurements of GPP and PAR and the average value of ecosystem LUE across data from all sites and years combined (1.76 g C MJ^{-1}). Estimates of k declined exponentially as LAI increased ($k = 0.30 + 1.28 \times e^{(-2.70 \times \text{LAI})}$, $r^2 = 0.48$, $P < 0.0001$, $n = 340$).

A simple linear regression with PARa calculated by varying k as an exponential function of LAI explained 62% of the variance in daily averages of GPP from each week (Table 2). The regression was fit using data from all grasslands, excluding data from the non-linear part of GPP–PARa curves in 2000 and 2001 for Mandan (slope = 1.66 g C MJ^{-1} for regression through the origin, $n = 340$). GPP–PARa curves remained strongly hyperbolic in 2000 and 2001 at Mandan when k was varied as a function of LAI ($r^2 = 0.61$ and 0.71 for 2000 and 2001). Inter-annual differences in GPP–PARa slopes, excluding data from non-linear relationships for Mandan, explained an additional 11% of the variance in grassland GPP and improved the r^2 of the regression model with PARa to 0.73. These trends provide evidence that ϵ_g varied significantly among years even after varying k as a function of LAI (Table 3). Means of ϵ_g values varied among years from 1.3 to 2.2 g C MJ^{-1} at Mandan, 1.6 to 1.9 g C MJ^{-1} at Nunn, and 1.4 to 1.9 g C MJ^{-1} at Woodward.

Slopes of linear regressions between GPP and LAI also differed significantly among site-years (Table 4). Inter-annual differences in GPP–LAI slopes explained 16% of the variance in GPP accounted for by a separate-slopes regression model with LAI ($r^2 = 0.63$, $n = 340$). Importantly, both seasonal means of ϵ_g and slopes of GPP–PARa relationships from each year and site increased linearly as GPP–LAI slopes increased ($r^2 = 0.36$, $P = 0.005$, and $r^2 = 0.66$, $P < 0.0001$, respectively, $n = 18$). The greater was GPP per unit of LAI during a given year, the greater was ϵ_g.

Table 4. Slopes of Relationships Between GPP (g C m^{-2} day^{-1}) and LAI Calculated for Each Year and Grassland

Source	GPP–LAI slope	Standard error
Intercept (0.3110)		
Mandan, North Dakota		
1995	6.49	0.55
1996	11.96	1.37
1997	11.70	1.32
1998	8.69	1.20
1999	19.21	1.95
2000	11.42	3.14
2001	5.86*	1.70
Nunn, Colorado		
1998	9.93	0.85
1999	7.48	0.74
2000	14.21	3.56
2001	8.06	0.95
Woodward, Oklahoma		
1999	5.48	0.41
2000	4.73	0.42
2001	7.03	0.59
2002	5.97	0.64
2003	3.85*	0.36
2004	3.98*	0.40
2005	4.59	0.43

Slopes labeled with an asterisk did not differ from the minimum slope observed.

Regulation of ϵ_g Calculated with Variable k

Environmental fluctuations explained little of the among-week variation in ϵ_g values calculated by varying k as a function of LAI. The ϵ_g was a weak linear function of evaporative deficit, the difference between potential and AET, across data from all years and sites combined ($r^2 = 0.06$, $P < 0.0001$, $n = 340$) and a positive linear function of ppt8 ($r^2 = 0.03$, $P < 0.0001$, $n = 340$). The ϵ_g was not correlated with T_a or LAI ($P = 0.39, 0.68$).

Seasonal means of ϵ_g declined as PET during May through July increased (Figure 5). The ϵ_g declined linearly as PET increased when analyzed using data from all grasslands and years. As estimated using this regression, ϵ_g decreased from 2.0 to 1.5 g C MJ^{-1} as PET increased from 350 to 650 mm. This decrease in ϵ_g at higher PET was 23% of the decrease observed when ϵ_g was calculated using a fixed k value. The correlation between ϵ_g and PET (mm) was significant only for Woodward when assessed with data from individual sites ($\epsilon_g = 3.341 - 0.003 \times \text{PET}$, $r^2 = 0.55$, $P = 0.03$, $n = 7$). None of the other factors we tested, including precipitation, evaporative deficit, the difference between PET and precipitation summed over various periods, and averages of LAI (Figure 6), T_a, and evaporative deficit for each growing season, explained inter-annual variation in ϵ_g among the 18 years of data from the three grasslands. Growing season means of ϵ_g values from each week increased as precipitation increased for each of the two grasslands for which variability in ϵ_g was greatest, however (northern and southern mixed prairie at Mandan and Woodward, respectively; <1 g C MJ^{-1} range in ϵ_g). Mean ϵ_g was a positive linear function of precipitation (mm) from October through January before each growing season for prairie at Mandan ($\epsilon_g = 1.432 + 0.004 \times \text{ppt}$, $r^2 = 0.48$, $P = 0.05$, $n = 7$) and of precipitation during March and April for prairie at Woodward ($\epsilon_g = 1.334 + 0.002 \times \text{ppt}$, $r^2 = 0.73$, $P = 0.0009$, $n = 7$).

DISCUSSION

Variability in ϵ_g

GPP increased linearly in most years as the amount of photosynthetically active radiation absorbed by plants (PARa) increased for three grasslands in the Great Plains of USA. A single linear regression through the origin of a plot of GPP versus PARa using data from all years and sites combined had a slope of 1.76 g C MJ^{-1} when the fraction of PAR absorbed by plants (f_{PARa}) was assigned a fixed value per grassland, as is common, and 1.66 g C MJ^{-1} when k was varied as a function of LAI across grasslands. Slopes of GPP–PARa regressions differed significantly among the 18 site-years of data, however, regardless of whether the value of k was fixed or variable. Inter-annual differences in GPP–PARa slopes accounted for 11–15% of the variance in GPP explained by linear regression on PARa. Seasonal means of ϵ_g decreased exponentially as LAI increased and linearly as PET increased when ϵ_g was derived using a fixed k value. Permitting k to vary as an exponential function of LAI reduced variability in calculated values of ϵ_g, eliminated the correlation between both weekly values and annual means of ϵ_g and LAI that occurred when k was fixed, reduced the slope of a negative linear regression between ϵ_g and PET, and clarified the predicted contribution of precipitation variability to inter-annual differences in ϵ_g. Mean ϵ_g was a positive linear function of precipitation from October through January before each growing season for northern mixed-grass prairie at Mandan and of precipitation during March and April for southern mixed-grass prairie at Woodward. Our data support three major conclusions. (1) PARa likely is underestimated at low LAI when f_{PARa} is calculated using a fixed k value, leading to an overestimation of ϵ_g at low LAI, much wider variation in ϵ_g among years and grasslands than is likely, and a negative exponential relationship between ϵ_g and LAI. (2) GPP of these grasslands may be predicted at the first order from variation in PARa using an average ϵ_g of 1.66–1.76 g C MJ^{-1}. (3) The dynamics of ϵ_g on these grasslands are better described by totals of PET and precipitation over months than by brief changes in air temperature and evaporative deficit. Inter-annual differences in sums of PET and precipitation thus could be used to improve grassland-specific estimates of ϵ_g for use in LUE algorithms.

Radiation Extinction Coefficient

The radiation extinction coefficient, k, often is assigned a fixed value to derive PARa and ϵ_g from CO_2 flux measurements and in canopy photosynthesis models (for example, Ruimy and others 1999; Turner and others 2003). A fixed k value may be appropriate for estimating PARa of closed canopies, although it has been shown that k declines as LAI increases even in well-developed stands of monocultures (Tahiri and others 2006; Irmak and Mutiibwa 2008). The assumption that k is fixed is more problematic for grasslands and other ecosystems on which LAI is small and varies greatly among sites and years. The seasonal average of LAI varied by an order of magnitude among years and the three grasslands we studied (LAI range 0.12–1.15). From detailed measurements in shortgrass steppe, Nouvellon and others (2000a) found that the k value for diffuse and total radiation decreases as LAI increases. Consequently, Nouvellon and others (2000a) concluded that PARa may be significantly underestimated (and, ϵ_g overestimated) using a fixed k value when LAI is small. Similarly, Irmak and Mutiibwa (2008) showed that k of a maize canopy declined exponentially at LAI greater than 1. Daily average values of k for maize were linearly correlated with the natural logarithm of LAI, ln(LAI), where $k = -0.439 \times \ln(\mathrm{LAI}) + 1.01605$. We found a similar pattern of logarithmic decay in the extinction coefficient of grassland canopies as LAI increased. By contrast, calculations of GPP were largely insensitive to change in the k parameter for a wide range of vegetation in arctic landscapes (Shaver and others 2007).

Grassland ϵ_g

GPP of mixed-grass prairie and shortgrass steppe may be predicted at the first order from variation in PARa using $\epsilon_g = 1.66$ g C MJ^{-1} (variable k) or 1.76 g C MJ^{-1} (fixed k). GPP could be estimated more closely using the mean value of ϵ_g for each site (1.86, 1.75, and 1.56 g C MJ^{-1} for Mandan, Nunn, and Woodward, respectively, when determined using variable k). Similar values of ϵ_g have been reported for other grasslands in the Great Plains of North America. Yuan and others (2007) calculated a ϵ_g of 1.38 g C MJ^{-1} for grassland in south-central Kansas, USA, whereas Turner and others (2003) reported a mean ϵ_g of 1.7 g C MJ^{-1} for the June–September period for tallgrass prairie in north-eastern Kansas. Schwalm and others (2006) found that ϵ_g averaged 3.64 g C MJ^{-1} for the growing season for mixed-grass prairie in Canada.

Slopes of regressions between GPP and PARa differed among years, evidence that inter-annual differences in LUE contributed to the overall variance in ϵ_g. Growing season means of midday ϵ_g also varied substantially among years in a boreal forest (Drolet and others 2008). Contrary to our prediction, however, inter-annual differences in GPP–PARa slopes explained a similar fraction of variance in GPP whether the k value was fixed or varied as a function of LAI (15 vs. 11%).

Inter-annual variation in ϵ_g was correlated with year-to-year differences in precipitation and PET over periods of 2 or more months before or early during each growing season. Both greater precipitation and a decrease in the environmental demand for water (PET) increased mean ϵ_g, presumably by increasing or conserving soil water content early in the growing season. Within-season patterns of ϵ_g also were regulated by water availability. Precipitation summed for November through February was low during the 2000 and 2001 growing seasons at Mandan when GPP–PARa relationships were hyperbolic. A hyperbolic GPP–PARa relationship implies that ϵ_g (GPP/PARa) decreased as PARa increased. Similarly, Flanagan and others (2002) reported light saturation of GPP on northern temperate grassland during years of average and below average precipitation. The ϵ_g of a shortgrass ecosystem was lowest during a year in which water limitation was greatest (Nouvellon and others 2000b), whereas ϵ_g of a boreal aspen forest declined as the mean of soil water content declined (Barr and others 2007).

The mechanism by which greater precipitation and lower PET stimulated ϵ_g is more difficult to discern with our data. We can say definitively only that neither factor increased ϵ_g by increasing LAI, at least when ϵ_g was calculated using variable k values. Increasing annual precipitation increased seasonal means of GPP on these grasslands, apparently by increasing LAI and PARa. Similarly, GPP correlated positively with LAI, which, in turn, increased as soil water content increased on both northern temperate grassland and annual grassland (Flanagan and others 2002; Xu and Baldocchi 2004). Inter-annual differences in ϵ_g on Great Plains grasslands resulted from differences in GPP at a given LAI rather than from differences in LAI, however. Mean ϵ_g for the season was greater during years when GPP at a given LAI was high than low. We interpret this trend to mean that ϵ_g varied among years because rates of photosynthesis per unit of leaf area varied in response to inter-annual differences in precipitation and PET. Water availability affects leaf photosynthesis both directly by influencing photosynthetic capacity and indirectly by affecting stomatal conductance.

It is important to recognize that relationships between seasonal means of ϵ_g and both precipitation and PET differed when analyzed for each grassland separately. Climatic variables useful for predicting variability in ϵ_g across grasslands did not necessarily account for variability on a given grassland. Inter-annual variability in ϵ_g, precipitation, and PET was smaller for a given ecosystem than across the grasslands we studied. We simply may not have been able to detect an effect of water availability or evaporative demand on ϵ_g given the limited variability in measurements from a given site. Alternately, photosynthesis and ϵ_g may respond differently to changes in precipitation and PET among grasslands because vegetation differs among sites. The contribution of C_4 species to LAI and total biomass increases from north to south in these grasslands, for example (Sims and others 1978). Photosynthesis often is less sensitive to water limitation among co-occurring C_4 than C_3 species of a given growth form (Chapin and others 2002). ''Site'' was the most important variable of those considered by Schwalm and others (2006) in explaining variability in ϵ_g among ecosystems in Canada. The ϵ_g may have differed among sites partly because vegetation differed among sites.

The typical approach of using short-term changes in the environment to describe daily or weekly variation in ϵ_g (for example, Schwalm and others 2006) may not be effective for ecosystems for which mean ϵ_g differs among years. Indeed, we found that week-to-week changes in air temperature, evaporative deficit, and recent precipitation accounted for little of the variability in grassland ϵ_g. Rather, our results support the use of PET during spring or precipitation received before each season to account for inter-annual differences in the values of ϵ_g used to calculate GPP. For example, GPP values calculated by multiplying the daily mean of PARa for each week by ϵ_g averaged across years for Mandan (1.86 g C MJ^{-1}) explained 63% of the variance in observations of GPP (regression through the origin; $n = 125$). The product of PARa per week and ϵ_g estimated for each year as a function of precipitation explained 78% of the variance in GPP at Mandan.

Our results also imply that greater attention be given to defining seasonal and inter-annual dynamics of the extinction coefficient for ecosystems with low LAI. Improving our understanding of how k varies with changes in LAI and other factors will improve estimates of ϵ_g that are derived from flux measurements and used in canopy photosynthesis models.

ACKNOWLEDGMENT

Douglas Johnson and Lewis Ziska provided helpful reviews of the manuscript.

REFERENCES

Angell R, Svejcar T, Bates J, Saliendra NZ, Johnson DA. 2001. Bowen ratio and closed chamber carbon dioxide flux measurements over sagebrush steppe vegetation. Agric For Meteorol 108:153–61.

Barr AG, Black TA, Hogg EH, Griffis TJ, Morgenstern K, Kljun N, Theede A, Nesic Z. 2007. Climatic controls on the carbon and water balances of a boreal aspen forest, 1994–2003. Glob Chang Biol 13:561–76.

Chapin FS III, Matson PA, Mooney HA. 2002. Principles of terrestrial ecosystem ecology. New York, Berlin, Heidelberg: Springer. 436 p

Davidson EA, Janssens IA, Luo Y. 2006. On the variability of respiration in terrestrial ecosystems: moving beyond Q_{10}. Glob Chang Biol 12:154–64.

Drolet GG, Middleton EM, Huemmrich KF, Hall FG, Amiro BD, Barr AG, Black TA, McCaughey JH, Margolis HA. 2008. Regional mapping of gross light-use efficiency using MODIS spectral indices. Remote Sens Environ 112:3064–78.

Dugas WA, Heuer ML, Mayeux HS. 1999. Carbon dioxide fluxes over Bermuda grass, native prairie, and sorghum. Agric For Meteorol 93:121–39.

Flanagan LB, Wever LA, Carlson PJ. 2002. Seasonal and inter-annual variation in carbon dioxide exchange and carbon balance in a northern temperate grassland. Glob Chang Biol 8:599–615.

Frank AB. 2002. Carbon dioxide fluxes over a grazed prairie and seeded pasture in the Northern Great Plains. Environ Pollut 116:397–403.

Frank AB, Sims PL, Bradford JA, Mielnick PC, Dugas WA, Mayeux HS. 2001. Carbon dioxide fluxes over three Great

Plains Grasslands. In: Follett RF, Kimble JM, Lal R, Eds. The potential of US grazing lands to sequester carbon and mitigate the greenhouse effect. Boca Raton (FL): CRC Press. p 167–88.

Gilmanov TG, Tieszen LL, Wylie BK, Flanagan LB, Frank AB, Haferkamp MR, Meyers TP, Morgan JA. 2005. Integration of CO_2 flux and remotely-sensed data for primary production and ecosystem respiration analyses in the Northern Great Plains: potential for quantitative spatial extrapolation. Glob Ecol Biogeogr 14:271–92.

Gower ST, Kucharik CJ, Norman JM. 1999. Direct and indirect estimation of leaf area index, fPARa, and net primary production of terrestrial ecosystems. Remote Sens Environ 70:29–51.

Hui D, Luo Y, Katul G. 2003. Partitioning interannual variability in net ecosystem exchange between climatic variability and functional change. Tree Physiol 23:433–42.

Irmak S, Mutiibwa D. 2008. Dynamics of photosynthetic photon flux density and light extinction coefficient to assess radiant energy interactions for maize canopy. Trans ASABE 51:1663–73.

Kiniry JR, Burson BL, Evers GW, Williams JR, Sanchez H, Wade C, Featherston JW, Greenwade J. 2007. Coastal bermudagrass, bahiagrass, and native range simulation for diverse sites in Texas. Agron J 99:450–61.

Nouvellon Y, Bégué A, Moran MS, Seen DL, Rambal S, Luquet D, Chehbouni G, Inoue Y. 2000a. PAR extinction in shortgrass ecosystems: effects of clumping, sky conditions and soil albedo. Agric For Meteorol 105:21–41.

Nouvellon Y, Seen DL, Rambal S, Begue A, Moran MS, Kerr Y, Qi J. 2000b. Time course of radiation use efficiency in a shortgrass ecosystem: consequences for remotely sensed estimation of primary production. Remote Sens Environ 71:43–55.

Polley HW, Mielnick PC, Dugas WA, Johnson HB, Sanabria J. 2006. Increasing CO_2 from subambient to elevated concentrations increases grassland respiration per unit of net carbon fixation. Glob Chang Biol 12:1390–9.

Polley HW, Emmerich W, Bradford JA, Sims PL, Johnson DA, Saliendra NZ, Svejcar T, Angell R, Frank AB, Phillips RL, Snyder KA, Morgan JA. 2010a. Physiological and environmental regulation of interannual variability in CO_2 exchange on rangelands in the western United States. Glob Chang Biol 16:990–1002.

Polley HW, Emmerich W, Bradford JA, Sims PL, Johnson DA, Saliendra NZ, Svejcar T, Angell R, Frank AB, Phillips RL, Snyder KA, Morgan JA, Sanabria J, Mielnick PC, Dugas WA. 2010b. Precipitation regulates the response of net ecosystem CO_2 exchange to environmental variation on US rangelands. Rangel Ecol Manag 63:176–86.

Reichstein M, Falge E, Baldocchi D, Papale D, Aubinet M, Berbigier P, Bernhofer C, Buchmann N, Gilmanov T, Granier A, Grünwald T, Havránková K, Ilvesniemi H, Janous D, Knohl A, Laurila T, Lohila A, Loustau D, Matteucci G, Meyers T, Miglietta F, Ourcival J-M, Pumpanen J, Rambal S, Rotenberg E, Sanz M, Tenhunen J, Seufert G, Vaccari F, Vesala T, Yakir D, Valentini R. 2005. On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm. Glob Chang Biol 11:1424–39.

Ruimy A, Kergoat L, Bondeau A. 1999. Comparing global models of terrestrial net primary productivity (NPP): analysis of differences in light absorption and light-use efficiency. Glob Chang Biol 5:56–64.

Running SW, Nemani RR, Heinsch FA, Zhoa M, Reeves M, Hashimoto H. 2004. A continuous satellite-derived measure of global terrestrial primary production. Bioscience 54:547–60.

Schwalm CR, Black TA, Amiro BD, Arain MA, Barr AG, Bourque CP-A, Dunn AL, Flanagan LB, Giasson M-A, Lafleur PM, Margolis HA, McCaughey JH, Orchansky AL, Wofsy SC. 2006. Photosynthetic light use efficiency of three biomes across an east-west continental-scale transect in Canada. Agric For Meteorol 140:269–86.

Shaver GR, Street LE, Rastetter EB, Van Wijk MT, Williams M. 2007. Functional convergence in regulation of net CO_2 flux in heterogeneous tundra landscapes in Alaska and Sweden. J Ecol 95:802–17.

Sims PL, Singh JS, Lauenroth WK. 1978. The structure and function of ten western North American grasslands I. Abiotic and vegetational characteristics. J Ecol 66:251–85.

Stephenson NL. 1990. Climatic control of vegetation distribution: the role of the water balance. Am Nat 135:649–70.

Svejcar T, Angell R, Bradford JA, Dugas W, Emmerich W, Frank AB, Gilmanov T, Haferkamp M, Johnson DA, Mayeux H, Mielnick P, Morgan J, Saliendra NZ, Schuman GE, Sims PL, Snyder K. 2008. Carbon fluxes on North American rangelands. Rangel Ecol Manag 61:465–74.

Tahiri AZ, Anyoji H, Yasuda H. 2006. Fixed and variable light extinction coefficients for estimating plant transpiration and soil evaporation under irrigated maize. Agric Water Manage 84:186–92.

Turner DP, Urbanski S, Bremer D, Wofsy SC, Meyers T, Gower ST, Gregory M. 2003. A cross-biome comparison of daily light use efficiency for gross primary production. Glob Chang Biol 9:383–95.

Veroustraete F, Sabbe H, Eerens H. 2002. Estimation of carbon mass fluxes over Europe using the C-Fix model and Euroflux data. Remote Sens Environ 83:376–99.

Webb EK, Pearman GI, Leuning R. 1980. Correction of flux measurements for density effects due to heat and water vapor transfer. Q J Roy Meteorol Soc 106:85–100.

Wolf A, Saliendra N, Akshalov K, Johnson DA, Laca E. 2008. Effects of different eddy covariance correction schemes on energy balance closure and comparisons with the modified Bowen ratio system. Agric For Meteorol 148:942–52.

Xu L, Baldocchi DD. 2004. Seasonal variation in carbon dioxide exchange over a Mediterranean annual grassland in California. Agric For Meteorol 123:79–96.

Yuan W, Liu S, Zhou G, Zhou G, Tieszen LL, Baldocchi D, Bernhofer C, Gholz H, Goldstein AH, Goulden ML, Hollinger DY, Hu Y, Law BE, Stoy PC, Vesala T, Wofsy SC. 2007. Deriving a light use efficiency model from eddy covariance flux data for predicting daily gross primary production across biomes. Agric For Meteorol 143:189–207.