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The relative importance of light-use efficiency modifications from environmental conditions and cultivation for estimation of large-scale net primary productivity

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Abstract

Understanding spatial and temporal variation in net primary production (NPP), the amount of carbon fixed into biomass by vegetation, is a central goal of ecosystem ecologists. Optical remote sensing techniques can help address this need by providing accurate, consistent, and reliable approximations of photosynthetic activity at large scales. However, converting photosynthetic activity into NPP requires estimates of light-use efficiency, which has been shown to vary among vegetation types. In this study, we compare remotely sensed estimates of absorbed photosynthetically active radiation with ground-based NPP estimates to determine appropriate light-use efficiency values for grasslands and croplands. We contrast the performance of models with and without information about vegetation type and light-use efficiency downregulation due to unfavorable environmental conditions. Our results suggest that: 1) current models may include overestimates of grassland light-use efficiency; 2) including vegetation information in light-use efficiency calculations causes a dramatically better fit between ground-based and remotely sensed estimates of primary production; and 3) incorporating environmental downregulation to light-use efficiency yields only minor improvements, which may be a result specific to annual estimates in grassland and cropland systems. In addition, this study presents a regional dataset of ground-based primary production estimates that may prove useful for future studies.

Keywords: Net primary production; Light-use efficiency; Grasslands; Croplands; Remote sensing; Absorbed photosynthetically active radiation; Normalized difference vegetation index; Cultivation; Cropping

1. Introduction

Remotely sensed spectral reflectance data are unique in their ability to provide consistent large-scale observations that can be related to ecological phenomena (Roughgarden et al., 1991), including net primary productivity (NPP). NPP is related to plant photosynthetic activity and can be estimated from remotely sensed imagery by observing patterns of light absorption (Sellers et al., 1995). Consequently, remote sensing techniques that quantify light absorption have emerged as the primary source of large-scale NPP information, and constitute one of the few actual observations of carbon cycling processes at regional or global extents. Monteith (1972, 1977) developed methods for estimating plant productivity from observations of absorbed photosynthetically active radiation (APAR) and estimates of light-use efficiency (LUE):

$$\mathrm{NPP} = \mathrm{APAR} \times \mathrm{LUE} \quad (1)$$

where NPP is net primary productivity (gC m^{-2} $time^{-1}$ typically aboveground), APAR is absorbed photosynthetically active radiation (MJ m^{-2} $time^{-1}$) and LUE is light-use efficiency (gC MJ^{-1}).

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Regional and global scale NPP studies require accurate estimates of both APAR and LUE. Although spatial and temporal variations in APAR can be consistently quantified through remote sensing techniques (Sellers et al., 1992), photosynthetic efficiency is not yet generally assessable by remote sensing (but see Barton & North, 2001 and Boegh et al., 2002). LUE is known to exhibit both spatial variation across vegetation types (Gower et al., 1999; Turner et al., 2002) and temporal variation at individual sites (Campbell et al., 2001; Nouvellon et al., 2000). Consequently, generating valid representations of LUE is especially difficult in regions with substantial cropping because native vegetation and crops often have different LUE values (Gower et al., 1999), creating spatial heterogeneity not captured by the remotely sensed reflectance observations. A common approach is to incorporate information about vegetation type and/or temperature/water availability conditions in LUE calculation (e.g., Ruimy et al., 1994). One such technique is the Carnegie–Ames–Stanford Approach (CASA) model for estimating NPP from remote sensing data. CASA is a widely recognized NPP model that downregulates photosynthetic efficiency in response to short-term adverse temperatures or dry soil conditions (Field et al., 1995; Potter et al., 1993).

Our objectives in this study are: 1) to characterize the discrepancies between NPP estimates from the existing CASA model (with existing LUE values) and ground-based data; 2) to address these discrepancies by inverting Eq. (1) to estimate separate grassland and cropland LUE values for use in remote sensing NPP models; and 3) to use these results to quantify the importance of the environmental and crop type LUE modifications in grassland and cropland systems. Ground-based NPP was computed for cropland from harvest information reported by the USDA, and for native grasslands from information in the State soil geographic database. We explored native grassland LUE using C_3 and C_4 LUE reported by Lobell et al. (2002), but also independently derived LUE for all three vegetation types.

A recent study by Lobell et al. (2002) quantified cropland LUE for individual US counties by utilizing the temporal dynamics of satellite-derived APAR (from CASA) together with NPP estimated from USDA harvest statistics. Lobell et al. (2002) reported LUE values by county, and concluded that cultivated areas have different LUE than native vegetation and that those estimates can be used to improve large-scale estimates of NPP derived from remote sensing.

Our study differs in both objectives and methods from Lobell et al. (2002), and therefore provides additional confidence in the derivation of crop LUE. The major methodological difference is that we analyzed cropland LUE and NPP together with that of native ecosystems since our study region, the Great Plains, includes a mixture of native grasslands and croplands. By contrast, Lobell et al. included only cultivated pixels to estimate LUE. By comparing time series information about cropland production with remotely sensed light absorption information for multiple sites, Lobell et al. estimated spatial variability in LUE. In contrast, we incorporated native grassland production and used long-term mean variables of plant productivity and light absorption to compute one LUE value for the entire region. Other differences in methods include the assumption by Lobell et al. that belowground productivity is a constant proportion of aboveground productivity regardless of the crop, whereas we calculated belowground productivity as a crop-dependent flexible proportion of aboveground productivity based on published carbon allocation ratios. Comparison of the results from these two approaches can provide valuable validation of the resultant LUE estimates.

2. Methods

2.1. Study site

We conducted this study in the U.S. Great Plains (Fig. 1), a region ideal for this study because it contains a wide range of cultivation intensities, and native vegetation is primarily grassland. Land use is dominated by grazed native grassland and cropland. Precipitation occurs primarily in the summer and mean annual precipitation ranges from less than 400 mm in the west to approximately 1000 mm in the east. Mean annual temperature ranges from 3 to 21 °C from north to south (Lauenroth & Burke, 1995).

Counties were included in this study based on availability of range site production data from the USDA Natural Resource Conservation Service's (NRCS) STATSGO data-

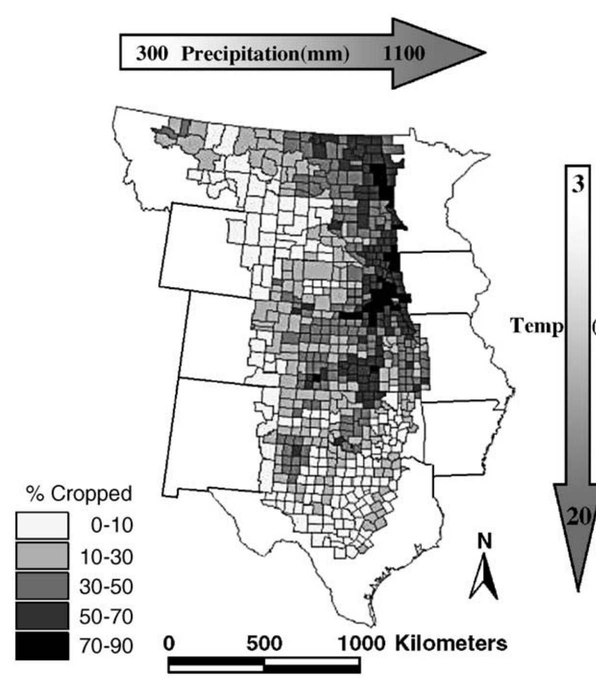

Fig. 1. Counties within the U.S. Central Great Plains region used in this study, their percent cropped area, and temperature and precipitation gradients.

base (SCS, 1976) and vegetation type as defined by Kuchler (1964). STATSGO provides production values only for states to the west of and including the Dakotas, Nebraska, Kansas, Oklahoma and Texas. Within this area we included the 630 counties that historically contained at least 70% of the following vegetation types: northern mixed grass prairie, shortgrass prairie, tallgrass prairie, tallgrass savanna, southern mixed grass prairie, desert savanna and floodplain forests. We collected USDA harvest and remote sensing data for the years 1990–1998.

2.2. Ground-based estimates of NPP

To quantify county-level productivity from ground-based measurements, we assumed all non-cultivated areas were native grassland, and considered each county as a mixture of cultivated areas and native grasslands.

2.2.1. Grasslands

In native grassland areas, we utilized data from the STATSGO database to compute aboveground net primary productivity (ANPP). NRCS divided each western state into range sites (several sites per county), and measured range site production, defined as ANPP (Joyce et al., 1986). We overlaid a county map over the range site production map and calculated the area-weighted average range site production value for each county. Estimating native belowground net primary productivity (BNPP) is more difficult than estimating ANPP (Lauenroth, 2000). Consequently, no empirical datasets for regional BNPP exist. However, Gill et al. (2002) reasoned that BNPP can be estimated as a function of maximum yearly belowground biomass (BGB), maximum proportion of BGB that is alive during the year (liveBGB/BGB), and root turnover (T) according to the equation:

$$\mathrm{BNPP} = \mathrm{BGB}\left(\frac{\mathrm{liveBGB}}{\mathrm{BGB}}\right)T. \tag{2}$$

Gill et al. (2002) used these relationships along with pairs of BNPP and ANPP from published studies to generate equations to predict BNPP from ANPP and temperature in grasslands. Their results indicate that BGB and liveBGB/BGB can be estimated from aboveground biomass (AGBIO: roughly equivalent to ANPP and estimated from ANPP) as:

$$\mathrm{BGB} = 79\mathrm{AGBIO} - 33.3(\mathrm{MAT} + 10) + 1289$$
$$R^2 = 0.55 \quad n = 52 \tag{3}$$

$$\frac{\mathrm{liveBGB}}{\mathrm{BGB}} = 0.6. \tag{4}$$

According to Gill and Jackson (2000), root turnover can be estimated from mean annual temperature (MAT) as

$$T = 0.2884e^{0.046\times\mathrm{MAT}} \quad R^2 = 0.48 \quad n = 71 \tag{5}$$

2.2.2. Croplands

To estimate NPP in cropped areas, we utilized acreage and economic yield data from the USDA National Agricultural Statistics Service (NASS) for the years 1990–1998 (NASS, 1998). Harvest yield (i.e., bushels or tons) were translated into ANPP and BNPP by using harvest index values (ratio of biomass harvested to total aboveground biomass) and resource allocation ratios (ratio of aboveground productivity to belowground productivity), respectively (e.g. Prince et al., 2001; Zheng et al., 2003). We used published harvest index values (Bradford et al., 2005) to calculate ANPP for cultivated areas following Prince et al. (2001).

2.2.3. Combining grassland and cropland NPP at the county level

At the county level, we estimated BNPP using county-specific allocation ratio and multiplying it by ANPP estimates (both from remotely sensed estimates and crop statistics). To derive allocation ratios for each county, we used published ANPP and BNPP values for crops to determine allocation ratios for cropped areas (Bradford et al., 2005), and assumed that uncultivated areas were native vegetation. Cultivated area was determined from USDA crop harvest statistics (NASS, 1998). Within each county, we estimated aboveground NPP (ANPP), belowground NPP (BNPP), and overall NPP (sum of ANPP+BNPP) for both cultivated areas and native grasslands. Ground-based estimates of whole-county NPP were calculated as the area-weighted average of NPP from cultivation and NPP from native grasslands on the remainder of the county.

2.3. Satellite-derived NPP

For our initial comparison between remotely sensed NPP and ground-based NPP we used the CASA model, with a minor modification, to estimate NPP for the years 1990–1998. The CASA model uses semimonthly measurements of the normalized difference vegetation index (NDVI) from NOAA's Advanced Very High Resolution Radiometer (AVHRR) to measure FPAR. NDVI has been strongly correlated with the fraction of absorbed photosynthetically active radiation (FPAR) in native vegetation (Goward & Huemmrich, 1992; Goward et al., 1994; Law & Waring, 1994) as well as crops (Daughtry et al., 1983; Gallo et al., 1985). Monthly values of FPAR were combined with incoming PAR to estimate monthly APAR. CASA represents LUE as a single global maximum value that is "down-regulated," or reduced during times of unfavorable temperature or water availability. Monthly LUE was determined as:

$$E = \mathrm{LUE}^{*}T_1T_2W \tag{6}$$

where LUE* is the maximum photosynthetic efficiency, T_1 and T_2 are reduction factors representing monthly deviations from site-specific optimal temperature and from 20 °C, respectively, and W represents monthly reduction in LUE due to low soil moisture as determined by a soil water model (Field et al., 1995; Potter et al., 1993).

We used CASA results described in Hicke et al. (2002) for 1990–1998. The NDVI data set has a spatial resolution of 8 km and was processed by Tucker et al. (2001) to minimize contamination by changes in orbital parameters, atmospheric conditions, and sensor differences. Solar radiation and temperature data were taken from the National Centers for Environmental Prediction reanalysis (Kistler et al., 2001), and the precipitation data set was produced by the Global Precipitation Climatology Project (Huffman et al., 1997). The climate data sets varied temporally in conjunction with NDVI and were spatially interpolated from 2.5° to the NDVI pixel locations.

2.4. Structure of cases representing LUE

To characterize discrepancies between CASA and ground-based data, we modified CASA NPP to represent LUE* as an area-weighted average of native area, C_3 cropland area and C_4 cropland area:

$$\mathrm{LUE}^* = N\mathrm{LUE}_N + C_3\mathrm{LUE}_3 + C_4\mathrm{LUE}_4. \tag{7}$$

LUE_N is the LUE for native vegetation, LUE_3 and LUE_4 are photosynthetic efficiency values of 0.29 gC MJ^{-1} for C_3 croplands and 0.66 gC MJ^{-1} for C_4 croplands reported by Lobell et al. (2002), who estimated these values by comparing time series of CASA NPP and cropland NPP estimated from USDA NASS yields. N, C_3 and C_4 were the area proportions within the county of native vegetation, C_3 cropland and C_4 cropland, respectively.

This initial analysis included two separate values of LUE for native vegetation. In the first version, we used the maximum LUE value of 0.405 gC MJ^{-1} employed by Hicke et al. (2002) ("CASA" case; Table 1). In the second version ("CASA new native") we determined the native vegetation LUE by finding the native LUE value that minimized squared errors between ground-based and CASA NPP for the 158 counties with less than 10% cultivation. For both approaches, we utilized the values of Lobell et al. for C_3 and C_4 LUE.

To examine how modifications to LUE from environmental (temperature and soil moisture) conditions and cropping practices impact the ability of remotely sensed techniques to measure county-level NPP, we formulated four cases that estimate NPP using Eq. (1) with varying methods for representing LUE (Table 1). To assess the influence of variations in sensitivity to cropping practices, one case uses a single value of LUE for the entire county (Table 1: "single LUE"), one case calculates LUE as a spatially weighted average of the cropped and native areas within the county (Table 1: "Cropped and grasslands"), and one case calculates LUE as a weighted average of native vegetation area, C_3 cropped area and C_4 cropped area (Table 1: "C_3 crops, C_4 crops and grasslands"). To examine the importance of limiting LUE based on environmental conditions, one case calculates separate LUE as a weighted average of native vegetation area, C_3 cropped area and C_4 cropped area but assumes constant LUE through time (Table 1: "No downregulation").

Unlike the two cases mentioned above that utilize existing LUE estimates ("CASA" and "CASA new native" cases), all the LUE values in these final four cases were

Table 1
Models for calculating NPP from NDVI-derived APAR and LUE values with statistically determined LUE values and standard errors by vegetation type for the CASA model, the CASA model with statistically determined native LUE, and other models with and without environmental LUE limitation and NPP estimates by county for STATSGO/crop data

Case	LUE representation		LUE estimation results			R^2	NPP (gC $\mathrm{m}^{-2}\mathrm{yr}^{-1}$)			Total PgC yr^{-1}
	Environmental limitation	Cultivation information	Vegetation Type	Estimate	SE		Mean	Min	Max	
CASA	Yes	Area in C_3 and C_4 crops	Grasslands	0.405	NA*	0.506	425.1	210.2	645.6	0.705
			C_3 crops	0.29	NA*					
			C_4 crops	0.66	NA*					
CASA with new grasslands	Yes	Only counties with <10% cultivation	Grasslands	0.246	0.002	0.8031	308.5	127.6	613.6	0.496
			C_3 crops	0.29	NA*					
			C_4 crops	0.66	NA*					
Single LUE	Yes	None	All vegetation	0.301	0.003	0.279	316.7	156.5	482.4	0.531
Cropped and grasslands	Yes	Total area cropped	Grasslands	0.219	0.004	0.671	318.6	113.4	516.3	0.512
			Cultivated	0.498	0.007					
C_3, crops C_4 crops and grasslands	Yes	Area in C_3 and C_4 crops	Grasslands	0.234	0.003	0.842	319.9	121.5	0.705	0.508
			C_3 crops	0.332	0.009					
			C_4 Crops	0.770	0.013					
No downregulation	No	Area in C_3 and C_4 crops	Grasslands	0.150	0.002	0.793	318.7	143.6	682.9	0.512
			C_3 crops	0.231	0.007					
			C_4 crops	0.548	0.009					
Ground Data							318.4	128.7	749.2	0.507

Values reported are coefficients of determination for comparisons between predicted and ground-based NPP, mean, min and max county NPP as well as regional NPP.

* These LUE values are based on previous studies rather than estimated in this study, so standard error values are not available.

determined from the data by minimizing least squared errors between satellite-derived (based on APAR) and ground-based NPP. Following Eq. (1), we incorporated ground-based county NPP (STATSGO/USDA crop harvest) and NDVI-derived APAR in a linear regression to determine the LUE as the slope of the fitted line. For the case with a single LUE value, ground-based NPP is the independent variable, APAR is the dependent variable, and LUE is the value for the slope that minimizes squared errors (see Eq. (1)). For the cases with multiple LUE values, county area in different vegetation types (Native, C_3, C_4) are the independent variables and LUE values are the coefficients that minimize squared errors according to the equations:

$$\frac{\mathrm{NPP}}{\mathrm{APAR}} = N\ \mathrm{LUE}_N + \mathit{Cult}\ \mathrm{LUE}_{cult} \tag{8}$$

$$\frac{\mathrm{NPP}}{\mathrm{APAR}} = N\ \mathrm{LUE}_N + C_3\ \mathrm{LUE}_3 + C_4\ \mathrm{LUE}_4 \tag{9}$$

where cult is the proportion of the county in cultivation and $\mathrm{LUE}_{\mathrm{cult}}$ is the calculated light-use efficiency for cultivated areas. We used the REG procedure with no intercept in SAS Version 8.0 (SAS, 1999) to perform these regressions with mean NPP, APAR and land use data from 1990–1998. We judged the accuracy of each case using coefficients of determination (R^2) and root mean square errors (RMSE).

3. Results

Our county-level estimates of NPP based on measured grassland productivity and crop harvest statistics averaged 318 gC m^{-2} $yr^{-1}$and ranged from 129 to 749 gC m^{-2} yr^{-1}. Over the entire U.S. Great Plains region, these values sum to 0.507 PgC yr^{-1}. The strongest spatial pattern is generally increasing NPP from West to East corresponding to the patterns of annual precipitation and consistent with previous studies (Epstein et al., 1997; Lauenroth et al., 1999; Sala et al., 1988). Our NPP values are similar to those of Prince et al. (2001), who also used crop statistics to estimate production for counties in the eastern part of this region (Fig. 2).

The version of CASA utilizing a maximum native LUE of 0.405 gC MJ^{-1} (“CASA” case) predicted higher county NPP than ground-based NPP from STATSGO data and crop harvest statistics. Of the 630 counties, 580 had higher county-level NPP estimates from CASA, whereas only 50 had higher estimates from ground-based measurements (Fig. 3: CASA). For the entire region, the difference between CASA and ground-based NPP estimates is 0.198 PgC yr^{-1} (Table 1). To provide an idea of the magnitude of this difference and therefore the opportunity for improvement in large-scale NPP estimation, the best estimates of the net carbon sink (the difference between the net carbon fixed by vegetation (NPP) and the release of carbon to the atmosphere through processes such as decomposition) for the conterminous US is 0.3–0.6 PgC yr^{-1} (Pacala et al., 2001).

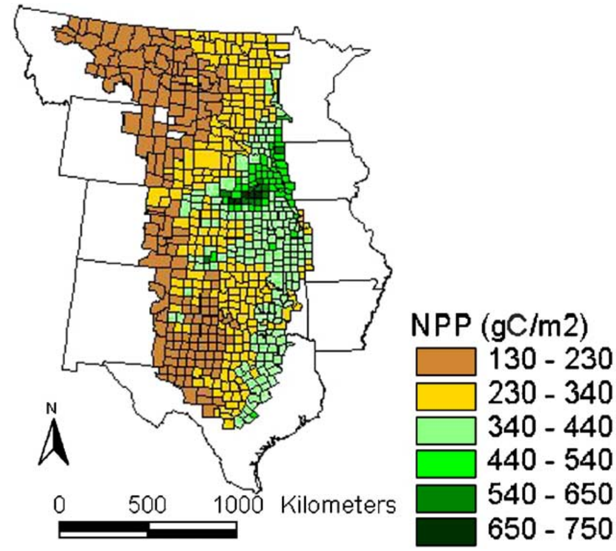

Fig. 2. Map of NPP estimates from ground-based data for the U.S. Great Plains.

Differences between CASA and ground-based estimates were negatively related to cropping intensity. Although the CASA model was originally calibrated on NPP measurements from multiple biomes, including native grasslands (Potter et al., 1993), counties with very low cropping (and hence a high proportion of native grassland) showed a consistent positive difference between CASA and ground-based estimates. Counties with higher levels of cropping, on the other hand, had lower, and in some counties negative, differences between CASA and ground-based NPP estimates. The better fit between CASA and ground-based NPP in heavily cropped counties suggests that published cropland LUE values from Lobell et al. (2002) are more accurate than the LUE used for native vegetation (Table 1).

For the “CASA new grasslands” case, we calculated an optimum native vegetation LUE estimate of 0.246 gC MJ^{-1} (Table 1), substantially lower than the LUE value of 0.405 gC MJ^{-1} that was calibrated from measurements in multiple ecosystems and originally utilized in CASA (Potter et al., 1993). This difference accounted for much of the discrepancy between CASA NPP estimates and ground-based NPP estimates. The case using the derived native grassland LUE dramatically improved the fit between predicted and observed NPP estimates (Table 1 and Fig. 3: “CASA new grasslands”).

When we represented LUE as a single value for all vegetation types, we estimated maximum LUE to be 0.301 gC MJ^{-1} (Table 1 and Fig. 3: “Single LUE”). Representing county LUE as an area-weighted average of native grassland and cultivated areas (Table 1 and Fig. 3: “Cropped and grasslands”) produced maximum LUE estimates for native and cultivated areas of 0.218 and 0.498 gC MJ^{-1}, respectively. When we represented LUE as a function of native grassland area, C_3 cropland area and C_4 cropland area (Table 1 and Fig. 3: “C_3 crops, C_4 crops and grasslands”),

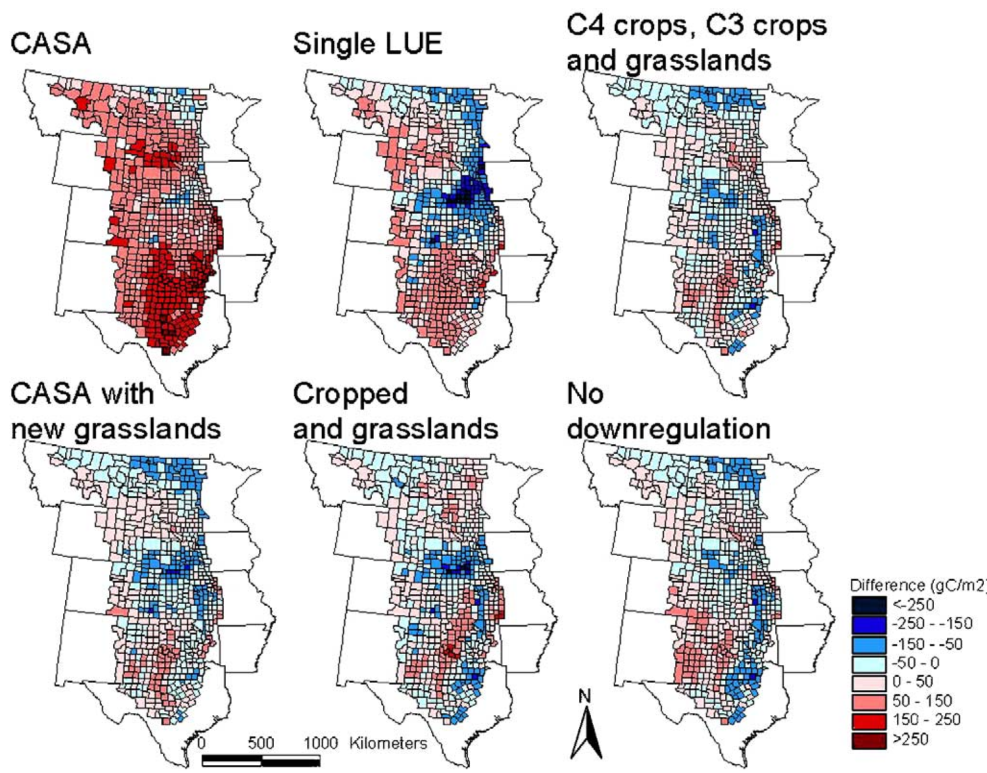

Fig. 3. Maps of differences between remotely sensed NPP estimates and ground-based NPP estimates for the U.S. Great Plains. Remotely sensed estimates of NPP (termed "cases" in the text) were generated from: 1) the CASA model ("CASA" case), 2) the CASA model with maximum LUE for native vegetation determined by least squares ("CASA new native"), 3) a single new LUE value determined by least squares ("Single LUE"), 4) separate new LUE values for cropland and native grasslands determined by least squares ("Cropped and grasslands"), 5) separate new LUE values for C_3 crops, C_4 crops and native grasslands determined by least squares ("C_3 crops, C_4 crops and grasslands"), and 6) separate new LUE values for C_3 crops, C_4 crops and native grasslands determined by least squares but not including environmental limitation of LUE ("No downregulation").

we found maximum LUE values of 0.234, 0.332 and 0.770 gC MJ^{-1}, respectively. As an alternative method, we computed LUE using only counties with less than 10% cultivation and found native maximum LUE value of 0.246 gC MJ^{-1}, very close to the native maximum LUE computed with all counties (0.234 gC MJ^{-1}). Not including environmental limitations yielded LUE estimates of 0.150, 0.231 and 0.548 gC MJ^{-1} for native areas, C_3 crops and C_4 crops, respectively (Table 1 and Fig. 3: "No downregulation").

4. Discussion

We observed a general pattern of highest LUE in C_4 crops, lower in C_3 crops and lowest LUE in grasslands; this pattern is also documented in previous studies (Gower et al., 1999; Ruimy et al., 1994). However, our LUE values, even those that include limitation due to temperature and soil moisture conditions, were generally lower than previously published LUE values determined at small scales. Gower et al. (1999) reviewed published studies of LUE and observed a range of 2.85–5.07 gC MJ^{-1} in C_4 crops, 1.02–5.2 gC MJ^{-1} in C_3 crops and 0.07–2.00 gC MJ^{-1} in grasslands. In a similar review, Ruimy et al. (1994) calculated a value of 2.07 gC MJ^{-1} for cultivated crops and 1.26 gC MJ^{-1} for grasslands. In our best NPP algorithm we observed LUE values of 0.77 gC MJ^{-1} in C_4 crops, 0.33 gC MJ^{-1} in C_3 crops and 0.23 gC MJ^{-1} in grasslands. The consistent discrepancy between our results and those from previous studies may be a consequence of different spatial scales, temporal durations, and methods of calculating LUE. Many previous studies have quantified LUE for short time periods (i.e., growing season or shorter) and at plot scales, whereas our study calculated annual LUE from NPP and APAR observations of entire counties, including non-vegetated or other low-productivity areas. In addition, our LUE values are based directly on FPAR and PAR and thus may be influenced by complications and potential biases in the process of estimating FPAR and PAR. Although seasonal patterns in FPAR estimates from remote sensing appear to closely approximate patterns observed on the ground (Turner et al., 2002), we utilized FPAR estimates based on biweekly maximum value composites. These composites may tend to slightly overestimate FPAR and consequently generate lower LUE estimates. Turner et al. (2003) found that large-scale PAR estimates (like those used in this study) can be higher than site-level PAR measurements, also possibly decreasing our LUE estimates.

Our case that utilized separate maximum LUE estimates for native, C_3 and C_4 crops (case "C_3 crops, C_4 crops and grasslands") produced values comparable to the LUE values from Lobell et al. (2002). The discrepancies between the results of Lobell et al. (2002) and our results are likely a consequence of differences in how we obtained our LUE estimates. First, we calculated LUE for all C_3 and C_4 crops, rather than specifically corn and wheat. Wheat is only modestly productive and may not display LUE representative of other C_3 crops. This may explain why our C_3 estimate is slightly higher than the wheat LUE of Lobell et al. Second, the approach of Lobell et al. (2002) of fitting LUE values to entire AVHRR pixels may produce slightly lower LUE estimates for C_3 and C_4 crops because each pixel may contain some native vegetation, which has lower LUE. Third, Lobell et al. utilized multiple NPP estimations during the year to compute one LUE per county; the values we used here were their means, which may result in differences. The differences in methods employed by these two approaches to estimating LUE makes comparisons between the approaches valuable for validation. This consistency in the estimated LUE values for specific land use types suggests that these values can be useful for calculating NPP from remotely sensed APAR data.

4.1. Importance of LUE modifications

Representing LUE as a single value yielded low R^2 and RMSE values (Fig. 4: "Single LUE"). This relatively poor performance is not surprising considering the substantial differences in observed LUE between native grasses and crops. Cultivated plants have been selected for consistent growth (e.g. Boukerrou & Rasmusson, 1990; Edmeades et al., 1999) and are often irrigated and/or fertilized, limiting the effect of resource limitation on cropland LUE and allowing some croplands to have higher LUE values than native grasslands. Counties with extremely heavy cropping had much higher NPP values from ground-based estimates than from remote sensing estimates for these algorithms, suggesting that the LUE used in these counties was too low.

Including information about the total area cropped in the calculation of LUE improved the relationship between predictions and ground-based observations compared to the algorithm that treated LUE as a single value (Fig. 4: "Cropped and grasslands"). We estimated lower native LUE and higher cropland LUE compared to the single LUE. This algorithm improved NPP predictions for counties with low productivity. Since unproductive counties tend to have low cropping intensity, these counties were primarily native grassland, were assigned lower LUE values, and were estimated to have low NPP values closer to the ground-based NPP estimates. Likewise, counties with heavy cultivation were assigned a high LUE value and subsequently had higher NPP predictions (compare the points with the highest NPP in Fig. 4 "Single LUE" with those in Fig. 4: "Cropped and grasslands"), again improving the fit with ground-based data. Despite this enhancement, NPP

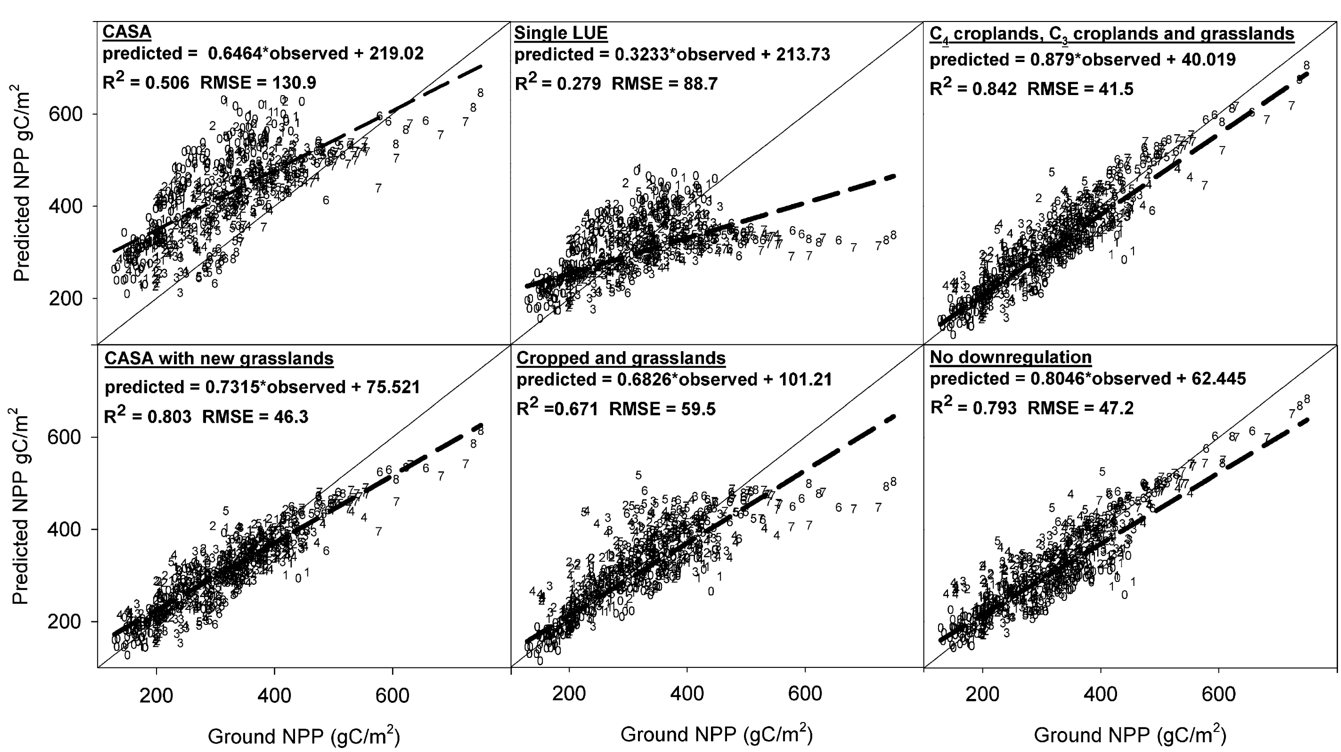

Fig. 4. Scatter plots of remotely sensed county NPP estimates for 6 LUE cases (described in Fig. 3) versus NPP estimates from ground data. Within the scatter plots each symbol represents a county, numerical values indicate cultivation intensity (0=0–10% cultivated, 1=10–20% cultivated, etc.) and solid lines are the 1:1 lines.

predictions for many counties with extremely heavy cultivation were still consistently lower than the ground-based estimates.

Representing LUE as an area-weighted average of native area, C_3 cropland and C_4 cropland produced the best relationship between NPP predictions and observations (Fig. 4: "C_3 crops, C_4 crops and grasslands"). The LUE value determined for C_4 crops is substantially higher than either the native or C_3 cropland LUE in this algorithm or the overall cropland LUE in "Cropped and grasslands". Since many of the extremely productive counties contain high proportions of corn, a common C_4 crop, this high LUE for C_4 crops elevates the predicted NPP for these counties to levels very close to the ground-based NPP.

Including environmental limitation improved NPP predictions, but the improvement was minor compared to the effect of separating cropland into C_3 and C_4 crops (Fig. 4: "No downregulation"). The marginal improvement as a result of down-regulators may be specific to grassland ecosystems. Modification of LUE for adverse environmental conditions may not be especially important for modeling NPP in grasslands because the satellite observations (NDVI/FPAR) capture most of the variability. Shallow rooting, short lifecycles and limited water storage capacity of grasses may cause tighter coupling between environmental conditions and light absorption (and thereby NDVI). Water is the primary limiting resource in grasslands (Noy-Meir, 1973), and grassland plants respond quickly to changes in water availability. Unlike coniferous trees, which maintain photosynthetic pigments throughout the winter, or deciduous trees, which use deep-rooted systems and water reservoirs in their trunks to maintain photosynthetic activity during brief droughts, grasses are quickly and dramatically impacted by soil moisture conditions. If the formation and degradation of photosynthetic pigments in grass leaves is closely linked to actual photosynthetic activity, then APAR observations will accurately measure NPP, minimizing the need to separately model LUE reduction due to environmental conditions. Alternatively, our perceived lack of importance of environmental LUE downregulation may stem from a mismatch between our annual (as opposed to monthly) comparisons between APAR and productivity (Montieth, 1972). Comparisons at shorter temporal scales might show more substantial improvement from environmental LUE downregulation (Field et al., 1995).

We note that by adjusting NPP derived from remotely sensed data to ground-based estimates, we may be compensating for inaccuracies in the NDVI/FPAR relationship in addition to LUE. The parameters of the linear NDVI/FPAR relationship were calculated assigning the tails of NDVI frequency distributions to low and high values of FPAR (see Los et al., 2000 for details). Thus, statistically modifying satellite-derived NPP to ground-based measures hides whether adjustments to FPAR or LUE are required.

5. Conclusions

Previous studies (e.g., Lobell et al., 2002) have determined that cultivated areas have LUE values different from native vegetation and that these differences influence remote sensing estimates of NPP. We found that the LUE value currently utilized in CASA produced consistently higher NPP estimates than our ground-based data in native grasslands, and to a lesser extent, in croplands. Calculating a new estimate for grassland LUE and combining it with C_3 and C_4 crop LUE values reported by Lobell et al. (2002) reduced the discrepancies between CASA NPP and ground-based NPP. In addition to this modification to CASA's LUE calculations, we formulated four other representations for LUE, compared NPP estimates using those representations with ground-based NPP estimates, and found that including vegetation information dramatically improved comparisons. Our statistically determined constant LUE value for the entire region was lower than the LUE used by CASA, accounting for CASA's general NPP overestimation in grasslands. Representing LUE as a mixture of native and cropped area indicated higher cropped LUE and even lower native LUE. When we divided LUE into three components (native vegetation, C_3 cropland and C_4 cropland), we found similarly low grassland LUE, intermediate values for C_3 cropland LUE and very high C_4 cropland LUE, consistent with previous results. Our best model among those that derived LUE values for all vegetation types, as indicated by the highest R^2 and lowest RMSE, resulted in similar values of C_3 and C_4 LUE as reported by Lobell et al. (2002) despite differences in methodology.

Comparisons between our algorithms for representing LUE suggest that grassland and cropland NPP predictions by remote sensing models are substantially improved by modifying LUE based on the total area cropped, and are further improved by including information about the proportion of C_3 and C_4 crops within the cropped area. Currently, many large-scale NPP estimation models that are based on remote sensing include environmental limitation, but do not include information about cropping practices. Based on our findings, we recommend that future studies examine LUE values for grassland ecosystems and modify LUE based on both cultivation information and environmental limitation. The regional dataset of ground-based estimates of aboveground and belowground primary production utilized in this study will prove valuable to future remote sensing and/or large-scale modeling efforts, and can be acquired by contacting the first author.

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