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Applying Improved Estimates of MODIS Productivity to Characterize Grassland Vegetation Dynamics

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Abstract

The efficacy of Moderate Resolution Imaging Spectroradiometer (MODIS)-derived vegetation productivity was tested in the grasslands of western North Dakota in terms of its ability to characterize fluctuations in aboveground green biomass and provide regional perspectives of interannual vegetation dynamics. To accomplish this task, we scaled plot-level observations of grassland biomass throughout the growing seasons of 2001 and 2002 using high-resolution satellite imagery and meteorological observations. Regionally scaled biomass measurements were compared with MODIS net photosynthesis (PSN_{net}) estimates at 3 times during the growing seasons of 2001 and 2002. The relationships between MODIS PSN_{net} estimates and scaled aboveground green biomass improved steadily during the progression of each growing season, and reached a maximum ($r^2 = 0.77$ and 0.57 in 2001 and 2002, respectively) near peak greenness. Aboveground green biomass was more tightly coupled in 2001 because of the relative abundance of green biomass compared with standing dead from the previous year. We characterized interannual variability in grassland vegetation through analysis of MODIS-derived net primary productivity (NPP) for the years 2001–2003. MODIS NPP estimates showed a significant decline ($P \leq 0.05$) from 2001 to 2003, partly induced by a significant decline ($P \leq 0.05$) in growing-season precipitation. The results indicate the reliability of productivity estimates for monitoring grassland biomass fluctuations is improved during years where plant growth conditions are more favorable. Additionally, MODIS data may be more useful for addressing administrative, rather than managerial, needs given the coarse resolution and regional perspective of the vegetation products.

Resumen

La eficacia de las estimaciones de la productividad de la vegetación derivadas del Espectroradiómetro de Imagen de Resolución Moderada (MODIS) se probó en pastizales del oeste de North Dakota, en términos de su capacidad para caracterizar las fluctuaciones de la biomasa verde aérea y proveer perspectivas regionales de las dinámicas interanuales de la vegetación. Para lograr esta tarea, escalamos observaciones a nivel de parcela de la biomasa del pastizal a través de las estaciones de crecimiento del 2001 y 2002 usando imágenes de satélite de alta resolución y observaciones meteorológicas. Las mediciones de biomasa escaladas regionalmente se compararon con estimaciones de la fotosíntesis neta de MODIS (PSN_{net}) en tres épocas durante las estaciones de crecimiento de 2001 y 2002. Las relaciones entre las estimaciones MODIS PSN_{net} y la biomasa verde aérea escalada mejoraron constantemente durante la progresión de cada estación de crecimiento y alcanzaron un pico casi máximo ($r^2 = 0.77$ y 0.57 en 2001 y 2002 respectivamente) de verdor. La biomasa verde aérea estuvo más fuertemente asociada en 2001 debido a la abundancia relativa de biomasa verde comparada con la biomasa muerta en el año previo. Caracterizamos la variabilidad interanual de la vegetación del pastizal a través del análisis de la productividad primaria neta (NPP) derivada del MODIS para los años 2001 al 2003. Las estimaciones de NPP del MODIS mostraron una disminución significativa ($P \leq 0.05$) del 2001 al 2003, parcialmente introducida por una reducción significativa ($P \leq 0.05$) de la precipitación durante la estación de crecimiento. Los resultados indican que la confiabilidad de las estimaciones de productividad para el monitoreo de las fluctuaciones de biomasa del pastizal se mejora durante los años en los que las condiciones para el crecimiento de las plantas son más favorables. Adicionalmente, los datos de MODIS pueden ser más útiles para abordar necesidades administrativas que de manejo, esto debido a su poca resolución y perspectiva regional de los productos de la vegetación.

Key Words: Little Missouri National Grasslands, remote sensing, production, photosynthesis

INTRODUCTION

Though ground-based reconnaissance is the most reliable method for assessing site-specific vegetative conditions, long-term planning and administrative needs may be more appropriately addressed by a synoptic, regional overview, which ground-based reconnaissance is unlikely to provide. Remote sensing offers a synoptic overview of vegetation productivity at

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Figure 1. Location of the Little Missouri National Grasslands (cross-hatched region) in North Dakota and the spatial arrangement of the zones of meteorological influence (Thiessen polygons).

regional scales and has been promoted as a diagnostic tool for these purposes (White et al. 1997; Sannier et al. 1998; Steininger 2000; Reeves et al. 2001; Tucker et al. 2001). The Moderate Resolution Imaging Spectroradiometer (MODIS) instrument potentially makes regional monitoring possible through generation of global, 8-day composites of net photosynthesis (PSN_{net}) and annual estimates of net primary productivity (NPP).

Few, if any, studies have evaluated the performance of regional MODIS vegetation-productivity estimates in grassland environments. Grassland environments make ideal test beds and simple laboratories for relating MODIS PSN_{net} (Running et al. 2004) to aboveground green biomass (AGGB) because large interannual fluctuations of AGGB are common, and dominance of herbaceous biomass makes data collection easy. In addition, herbaceous vegetation tends to respond more quickly to precipitation (Lauenroth 1979) than other types of vegetation. This makes aboveground biomass a logical attribute to relate with MODIS PSN_{net} for regional studies, though conceptually, MODIS primary-productivity estimates can only be quantitatively validated by comparison with flux tower measurements, such as in Heinsch et al. (2005).

A network of these towers, administered by AmeriFlux, exists in the United States (Baldocchi et al. 2001). AmeriFlux is a regional network of sites making measures of net

ecosystem exchange (NEE) of CO_2 between the biosphere and the atmosphere. From these measures, NPP and gross primary productivity (GPP) can be estimated for a site, which can be used to validate MODIS-derived NPP and GPP. However, tower-based estimates of productivity represent a spatial average of carbon flux over a tower footprint, the dimensions of which depend on wind speed, wind direction, surface roughness, and atmospheric stability (Turner et al. 2003). The variably sized, usually small ($< 1 \text{ km}^2$) footprint of flux towers, combined with low tower density in grassland environments, makes validation of MODIS products in rangeland environments challenging. Moreover, most management schemes rely more on biomass dynamics than carbon flux measurements.

Here we test the efficacy of the MODIS as a monitoring tool by comparing MODIS PSN_{net} with scaled AGGB and NPP to precipitation. First biomass observations were scaled for each of 12 mapping units in the Little Missouri National Grasslands (LMNG) for 2001 and 2002. Second, we quantified total precipitation from 1 January to peak greenness for each mapping unit in the LMNG for 2001–2002. Third, we compared time-integrated MODIS productivity estimates from 1 January through the composite period containing the date of AGGB prediction with scaled biomass observations. Finally, we characterized interannual variation of NPP in relation to differing amounts of growing-season precipitation.

MATERIALS AND METHODS

Study Area

Field data were collected in the LMNG located in North Dakota (Fig. 1). This 809 380-ha area is managed primarily by the U.S. Department of Agriculture (USDA) Forest Service as natural grazing lands for domestic and wild animals. Portions of the LMNG were converted to nearly homogenous stands of crested wheatgrass (*Agropyron desertorum* [Fisch. ex Link] Schult.) in the early to mid-1900s.

Because of the large geographic expanse and dominance of federal ownership, the LMNG provides a good opportunity for comparing measurements of AGGB to MODIS productivity estimates. Climate of the LMNG is continental and semiarid, and Cleland et al. (1997) provide a detailed description of the LMNG geoclimatic setting. Annual average precipitation varies from 360 to 410 mm, with 70% occurring between April and September (Whitman 1978). In 2001, the LMNG region was notably wetter during the growing season (1 April to 1 September) and drier in 2002 and 2003 than the 5-year mean (Fig. 2). Potential natural vegetation of the LMNG is typical of the mixed-grass prairie in the Northern Great Plains (Jensen et al. 2001) and is predominantly a wheatgrass–needlegrass (*Agropyron-Stipa*) association (Jensen et al. 2001). Dominant species include western wheatgrass (*Agropyron smithii* [Rydb.]), green needlegrass (*Stipa viridula* [Trin.]), needle and thread grass (*Stipa comata* [Trin. & Rupr.]), blue grama (*Bouteloua gracilis* [H.B.K.] Lag.) and threadleaf sedge (*Carex filifolia* Nutt.).

Data Collection

The primary purpose of obtaining the field measurements during the 2001 and 2002 growing season was to describe spatial and temporal trends in AGGB ($\text{kg} \cdot \text{ha}^{-1}$). We sampled selected grazing allotments representative of the different areas within the LMNG, which contained a range of biomass levels from nearly bare ground around prairie dog towns to heavily vegetated allotments. Due to time constraints and logistical considerations, slightly different methods for measuring and scaling AGGB were employed in 2001 and 2002.

Aboveground green biomass was measured during 3 time periods (27–31 May, 13–17 June, and 13–17 July) during the 2001 growing season in the LMNG. During the first, second, and third sampling periods, 145, 160, and 168 transects were sampled, respectively. Sites were selected based on federal ownership and accessibility and to provide an even geographical distribution across the LMNG. For each site, a transect was established perpendicular to and started at least 50 m from fence lines to avoid the influence of roads or channeled livestock trails that typically run along fence lines. Transect length was randomly determined and varied from 250 to 500 m. Beginning and ending locations for each transect were recorded with a global positioning system. At 25-m intervals, a 0.5-m^2 quadrat was clipped at 1-cm stubble height. Both living (green) and dead vegetation were separated and placed in paper bags. A total of 2 200 quadrats were clipped in the 2001 growing season. Following the 2001 data collection, we related transect averages within each grazing allotment to the Enhanced Thematic Mapper plus (ETM+) Normalized Difference Vegetation Index (NDVI) over the identical spatial domain. The NDVI is formulated as

$$\text{NDVI} = (\text{NIR} - \text{RED}) / (\text{NIR} + \text{RED}), \quad [1]$$

where NIR and RED are the spectral responses for the near-infrared and red wavebands, respectively. The NDVI is commonly related to biomass (Prince and Tucker 1986; Box et al. 1989; Wylie et al. 1995, 1996).

Our initial analyses indicated that we could improve the statistical relationship between plot data and NDVI at the allotment level by modifying our data-collection procedure during the 2002 field campaign. The mean allotment size for the LMNG is 342 ha, making it difficult to strike a balance between sufficient sampling intensity for a given allotment while sampling enough allotments to cover the range of variability expected across the differing environments within the LMNG. Based on this premise, we modified our sampling procedure for 2002, hoping that a pixel-based approach (3×3 pixel average NDVI vs. plot-level biomass) would provide a more accurate depiction of the range of variability within and between allotments that were sampled. Aboveground green biomass was measured in the 2002 growing season at 426 sites over 3 time periods (20–23 May, 14–17 June, and 10–13 July). During the first, second, and third sampling periods, 142, 148, and 136 transects were sampled, respectively. At each site, a sampling microsite (45×45 m) and an associated microsite center were established. The microsite center is a $15 \times 15\text{-m}$ area at the middle of each microsite. Microsites were homogeneous in species composition and biomass. This sampling scheme was designed to

Figure 2. Difference between 2001–2003 growing-season precipitation and the 50-year mean at 12 weather stations within and adjacent to the Little Missouri National Grasslands.

dovetail with Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) or ETM+ NDVI. The reason we used ASTER NDVI in 2002 is explained later under the “Procuring and Processing ASTER and ETM+ Imagery” section. Within each microsite center, aboveground biomass was clipped within 5 randomly located 0.5-m^2 quadrats in the same manner as in 2001. A total of 2 130 quadrats were clipped during the 2002 growing season. All herbaceous biomass collected was subsequently dried at 65°C for at least 48 hours and weighed. The average AGGB per site was calculated as the total dry weight multiplied by the percentage of green vegetation from each sampled quadrat during each sampling period for both years of the study.

Scaling Biomass Observations

Biomass observations were spatially scaled (aggregated) for comparison with MODIS vegetation-productivity estimates by relating AGGB to NDVI generated from ETM+ and ASTER for each period when biomass samples were obtained. For visible and NIR channels, ASTER has a spatial resolution of 15 m while ETM+ has a resolution of 30 m, and both sensors measure radiance in the identical RED wavelength ($0.63\text{--}0.69 \mu\text{m}$) and nearly identical NIR bands ($0.78\text{--}0.86$ and $0.75\text{--}0.79 \mu\text{m}$ for ASTER and ETM+, respectively).

Procuring and Processing ASTER and ETM+ Imagery

Three cloud-free level-1G ETM+ scenes (path 34/row 27) were acquired over the LMNG for 19 May, 22 June, and 22 July 2001. All scenes were registered to Universal Transverse Mercator (UTM) zone 13 North and exhibited less than 10% cloud cover. A dark-object subtraction was applied to reduce scattering effects. All scenes were cloud and water masked, coregistered, and converted from digital counts to radiance ($\text{W} \cdot \text{m}^{-2} \cdot \text{sr}^{-1} \cdot \text{nm}^{-1}$). To minimize between-scene variability, radiance values were converted to at-sensor reflectance as described by Markham and Barker (1986). Bands 3 (RED) and 4 (NIR) were subsequently transformed to NDVI (Eq. 1).

In 2002, no cloud-free ETM+ data were available, so instead we obtained 22 ASTER L2 surface-reflectance images

of the LMNG. These ASTER scenes collectively covered the temporal range of 13 May, 5 June, 30 June, and 9 July 2002. All 22 ASTER scenes were georegistered to UTM zone 13 North. NDVI was subsequently computed for each ASTER image. ASTER L2 surface reflectance data are radiometrically calibrated and atmospherically corrected. The advantage of ASTER surface reflectance data over ETM+ data is that they are immediately useful for quantifying biophysical traits of the earth's surface. Atmosphere-corrected sensor data provide a more reliable dataset for characterizing most vegetative traits (Turner et al. 1999). A disadvantage of ASTER data is the smaller spatial coverage (about 470 610 ha/scene) compared with that of ETM+ (about 4 900 000 ha/scene).

Building the Biomass-Scaling Models

A 30-m spatial-resolution image depicting grassland habitats throughout the LMNG was obtained from Jensen et al. (2001) and used to isolate the spectral response of grassland vegetation for creation of the aboveground biomass-scaling models. This included masking out woody and agricultural vegetation. Following the masking procedure, a series of tests were performed to establish the most robust relationship between biomass measurements and NDVI computed from either ASTER or ETM+. These tests included 1) pixel to sample point comparison, 2) average NDVI within each grazing allotment, 3) 7×7 - and 3×3 -pixel zonal mean for 2001 and 2002 data, respectively, and 4) average NDVI by zone of meteorological influence (described below).

The zonal mean is the arithmetic mean of the pixels within the 3×3 - or 7×7 -pixel window. We chose a 7×7 -pixel area surrounding each transect in 2001 and a 3×3 -pixel area around each microsite in 2002. The 7×7 -pixel kernel (210×210 m) was chosen because the average length of sample transects was about 200 m, while the 3×3 -pixel kernel was chosen because this ensures a ± 2 -pixel boundary around each microsite center in 2002. Another level of aggregation included spatially averaging NDVI within each grazing allotment. As a final method of relating biomass to NDVI, a zone of meteorological influence was established through creation of Thiessen polygons (Fig. 1) around weather stations found within and adjacent to the study area. Thiessen polygons were created using ArcInfo 7.0 (ESRI 2002). As demonstrated in Figure 1, a Thiessen polygon is drawn so that the lines are of equal distance between 2 adjacent points. Thiessen polygons are also referred to as Voronoi diagrams.

Ordinary least squares regression (Zar 1995) was used to evaluate statistical significance and the accuracy of the regression relationship between average biomass and average NDVI within each of these spatial domains. While spatially averaging all plots within each Thiessen polygon reduces the sample size available for analyses, it also reduces variability between geographically similar plots while emphasizing regional differences.

For each Thiessen polygon, daily precipitation and minimum and maximum temperature were obtained from the National Climate Data Center database of surface meteorology for the years 2001–2003. These data were screened such that if $> 5\%$ of the observations in any meteorological category were missing in any year, then the station was not used. This resulted in 12 complete stations and corresponding Thiessen polygons for 2001–2003 growing seasons (Fig. 1). We used stepwise re-

gression to determine the regression model for scaling biomass observations. The model initially included the meteorological variables and NDVI for each Thiessen polygon. A tolerance of 0.01 was selected for avoiding variables exhibiting a high degree of collinearity during the forward-stepping regression process.

Processing and Computing Improved MODIS Vegetation-Productivity Data

Collection 3 (Heinsch et al. 2003) land cover and collection 4 leaf-area index/fraction of photosynthetically active radiation (LAI/FPAR) data for the MODIS tiles H10 V04 and H11 V04 were obtained from the Earth Observing System Data Gateway for 2001–2003. Both the land cover and LAI/FPAR are 1-km^2 spatial resolution products. The primary productivity estimates used in this study were computed from the standard LAI/FPAR and land-cover products but used modified daily meteorological records and the updated biome properties look-up table found in Heinsch et al. (2003). The original meteorological data used for standard computation of MODIS productivity estimates comes from the Data Assimilation Office (DAO) (Atlas and Lucchesi 2000) and includes daily estimates of minimum and average temperature, solar radiation, and vapor-pressure deficit. These meteorological data are only available at $1.25^\circ \times 1^\circ$ spatial resolution. This ensures that, within the spatial extent of each DAO cell, every 1-km^2 MODIS pixel will inherit identical DAO characteristics. The disparate resolution of these inputs to the MODIS productivity algorithm produce noticeable and artificial boundaries in the end products, particularly the 8-day composite PSN_{net} . As a result, we spatially smoothed the DAO data using the method of Zhao et al. (2005), thereby taking out the artificial boundaries.

The results of the spatially smoothed DAO input on weekly PSN_{net} are noticeable in North Dakota and the region surrounding the LMNG (Fig. 3). Figure 3A depicts the artificial boundary caused from coarse DAO data, while Figure 3B portrays the results of the spatially smoothed DAO data and temporally filled LAI/FPAR.

In addition, due to clouds, we temporally filled the LAI/FPAR product where necessary. The LAI/FPAR product is ultimately derived from atmosphere-corrected surface-reflectance data and conveniently contains quality-assurance layers within each file. The quality-assurance layer provides a means of screening all pixels that are not desirable for analysis, either as a result of sensor and algorithm performance, atmospheric conditions, or cloud contamination. For this study, we only used the highest quality pixels.

Vegetation-Productivity Algorithm

Here we provide a synopsis of the vegetation-productivity algorithms but a complete derivation, including scientific basis and historical context, is provided in Running et al. (1999) and Heinsch et al. (2003).

For examining interannual variation in primary productivity we used NPP,

$$\text{NPP} = \sum (\text{PSN}_{\text{net}}) - R_g - R_m, \quad [2]$$

where NPP is the estimate of annual net primary productivity; R_m is the maintenance respiration of live cells in woody tissues

Figure 3. Comparison between standard Moderate Resolution Imaging Spectroradiometer-derived net photosynthesis (PSN_{NET}) (A) and the enhanced version that contains spatially smoothed meteorology and temporally filled leaf-area index/fraction of photosynthetically active radiation (B) Images are PSN_{net} ($kg \cdot C \cdot m^{-2}$) from composite period 185, 2001.

(Running et al. 2000); R_g is the annual growth respiration required to construct leaves, fine roots, and new woody tissues (Running et al. 2004); and PSN_{net} is the estimate of net photosynthesis for a 24-hour period. For this study, we used the improved PSN_{net} as described above to derive NPP data for 2001–2003.

Net photosynthesis is computed as

$$PSN_{net} = GPP - R_{lr}, \quad [3]$$

where GPP is the daily estimate of gross primary productivity, and R_{lr} is the 24-hour maintenance respiration of leaves and fine roots. Gross primary productivity is computed as

$$GPP = \varepsilon \cdot PAR \cdot FPAR, \quad [4]$$

where GPP is the 24-hour estimate of gross primary productivity ($kg \cdot C \cdot m^{-2}$), ε is the radiation use efficiency ($kg \cdot C \cdot MJ^{-1}$ photosynthetically active radiation [PAR]), and FPAR is the fraction of absorbed PAR. The FPAR used in this algorithm is a separate MODIS vegetation product, which is also freely available as an 8-day composite image (Myneni et al. 1997; Myneni et al. 2000).

All MODIS land products were converted from their native hierarchical data format to flat binary and reprojected from the sinusoidal projection to Lamberts azimuthal equal area (center of longitude -100° , reference latitude 45°). Following the reprojection, tiles were merged and scaled ($kg \cdot C \cdot m^{-2}$) to form a seamless representation of the study area. Primary-productivity estimates were spatially subset to include only grassland vegetation. The analysis mask for this process was derived from

MODIS land-cover type 2 data (Strahler et al. 1996). The MODIS land-cover mask indicated about 72% of the region was occupied by grassland vegetation. The Type 2 land cover is comparable with the International Geosphere-Biosphere Program global land-cover data set (Hansen and Reed 2000).

Analyzing Intra- and Interannual Productivity Dynamics

All MODIS grassland pixels were averaged within each Thiessen polygon to obtain a single mean estimate of time-integrated PSN_{net} from the start of the year to each date of biomass prediction. Net primary productivity was aggregated in a similar fashion. Because each Thiessen polygon was a different size, NPP means were computed on an area-weighted basis. The relationship between regionally scaled biomass measurements and MODIS PSN_{net} was determined using ordinary least squares regression in each of 3 sampling periods for the entire LMNG in 2001 and 2002. Detection of significant ($P \leq 0.05$) interannual differences between regionally averaged NPP means from 2001, 2002, and 2003 was accomplished using a 1-way analysis of variance and the Tukey test (Zar 1995) for separating means. Trends in NPP were compared with growing-season precipitation trends for the same spatial and temporal domain. The precipitation data used for this analysis were the same as those used for building the biomass-scaling models described above.

RESULTS AND DISCUSSION

Biomass-Scaling Models

No strong relationships were found between either ETM+ or ASTER NDVI and clipped plot biomass for any aggregation

Table 1. Relationship (r^2) between sample measures of aboveground green biomass and Enhanced Thematic Mapper plus (ETM+; 2001) and Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER; 2002) Normalized Difference Vegetation Index (NDVI). Dates are sample period midpoints.

Date	Zonal pixel mean ¹	Point in cell	Allotment mean	Thiesson polygon mean
2001				
28 May	0.11 ²	0.00	0.16 ²	0.49 ²
15 June	0.15 ²	0.26 ²	0.23 ²	0.62 ²
15 July	0.25 ²	0.20 ²	0.28 ²	0.81 ²
2002				
22 May	0.03	0.10	0.07	0.39 ²
16 June	0.21 ²	0.15 ²	0.25 ²	0.57 ²
12 July	0.28 ²	0.23 ²	0.22 ²	0.68 ²

¹In 2001, a 7×7 zonal mean was used. In 2002, a 3×3 zonal mean was used.

²($P \leq 0.05$).

method except the zone of meteorological influence (Thiesson polygons) (Table 1). The ETM+ NDVI explained from 49 to 81% of the variability of aboveground biomass in 2001. ASTER NDVI was less related to observed biomass than ETM+ and explained from 39 to 68% of the variability in regional biomass observations. The highest degree of association between biomass and NDVI occurred during the July sampling periods (near peak greenness) during both years of the study. Aboveground green biomass observations were obtained only 3 times during the growing seasons of 2001 and 2002. Thus, using clipped plot data, it is not possible to know exactly when peak greenness occurred throughout the LMNG, though, in each year, biomass observations were highest in July.

There are several likely reasons why there were weak linkages between NDVI and clipped biomass in all comparisons except the Thiesson polygons. First, while clipping remains the most objective method of measuring biomass on small plots, estimating the amount of green vegetation within a sampling quadrat is difficult. For example, what the human eye detects as green might, in reality, be nearly nonphotosynthetic, distorting the NDVI/green biomass relationship. This is because our sampling design required the observers to separate green from senesced vegetation. This begs the question “What shade of green indicates that the grass is photosynthetic or what shade of brown indicates the grass is senesced?” This perhaps highlights the need for new methods of data collection, such as ground-based radiometric measurements (i.e., a digital camera or radiometer). Second, especially at the end of the growing season, there might be a substantial amount of senesced vegetation within a plot frame of which the canopy resides over the top of relatively green vegetation. This green vegetation would be separated and weighed but, due to the effects of the senesced vegetation in the upper canopy, the NDVI signal would remain low. Finally, there is a poorer correlation between NDVI derived from upwelling radiance than between NDVI derived from atmosphere-corrected data and biomass (Shoshany et al. 1995; Turner et al. 1999), which would have only affected the 2001 scaling model because the ASTER data used in 2002 was received as surface reflectance rather than

Table 2. Results of stepwise regression for 2001 and 2002. Only the retained significant variables are summarized.¹ $n = 22$ for 2001 and $n = 21$ for 2002.

Model iteration ²	Adjusted R^2	SEE	Partial correlation coefficient	t -value ¹
2001				
1. ETM+ NDVI	0.81	5.40	0.90	9.55
2. gdd_{sum}	0.89	4.19	-0.66	-3.78
2002				
1. ASTER NDVI	0.82	5.66	0.89	9.80
2. gdd_{sum}	0.87	4.65	-0.60	-3.20

¹ $P < 0.05$.

²SEE indicates standard error of the estimate; ETM+, Enhanced Thematic Mapper; NDVI, Normalized Difference Vegetation Index; gdd_{sum} , summation of growing degree days; and ASTER, Advanced Spaceborne Thermal Emission and Reflection Radiometer.

digital counts. While we initially assumed that ASTER NDVI would be more closely related to AGGB, the presence of large amounts of senescent vegetation in 2002 meant ASTER NDVI was, in fact, less correlated with biomass.

Based on these findings, we proceeded to develop the biomass-scaling models as indicated in the “Methods.” The results of the forward-stepping regression procedure are shown in Table 2. This procedure resulted in models using only NDVI and thermal time (Table 2) of the form

$$BIOMASS_{AG01} = NDVI_{ETM+}(212.6) + gdd_{sum}(-0.003) - 33.8, \quad [5]$$

where $BIOMASS_{AG01}$ is the estimated AGGB within each Thiesson polygon in 2001, $NDVI_{ETM+}$ is the average ETM+ NDVI for a given polygon, gdd_{sum} is the summation of thermal time (TAVG_{daily} 0°C) from 1 January 2001 to the date of ground sampling, where TAVG_{daily} is the daily average temperature. In 2002, a similar model was constructed for scaling biomass observations,

$$BIOMASS_{AG02} = NDVI_{ASTER}(266.7) + gdd_{sum}(-0.009) - 57.9, \quad [6]$$

where $BIOMASS_{AG02}$ is the estimated AGGB within each Thiesson polygon in 2002 and $NDVI_{ASTER}$ is the average ASTER NDVI for a given polygon.

These models make sense biologically because they make use of thermal time, which controls the ontogenetic development (Baker et al. 1986; De Beurs and Henebry 2004) and NDVI as a surrogate for photosynthetically active leaf area (Choudhury 1987; Turner et al. 1999). Precipitation was not selected as a predictor variable in either year, due to the high colinearity with NDVI. In both years of the study, the scaling models were designed to estimate biomass for areas where biomass observations were not taken and for time periods as close as possible to the midpoint of each sample period.

Leave one out (LOO) cross-validation (Schumacher et al. 1997) proved that the scaling models worked sufficiently well for describing spatial patterns of vegetation throughout the grassland region (Fig. 4), though a higher degree of bias was observed in the 2002 model. In the LOO method, all data

Figure 4. Leave one out (LOO) cross validation results of the biomass-scaling models for 2001 and 2002. The predicted values come from Equations 5 and 6. MAE indicates mean absolute error; ●, May; ○, June; and △, July.

points, except 1, are iteratively used to build the predictive equation. The single point that is held out during each iteration is then used as the validation point.

Regionally scaled AGB produced at peak greenness was estimated as 1054 ± 36 (SEM) and 980 ± 44 (SEM) $\text{kg} \cdot \text{ha}^{-1}$ for 2001 and 2002, respectively. These values compare favorably with results from Hanson (1976), who reported an 11-year mean of $1\,012 \text{ kg} \cdot \text{ha}^{-1}$ in a similar grassland environment in Montana. The site evaluated by Hanson (1976) received an annual average of 330 mm of precipitation and had similar species composition to the current study area.

Comparing Net Photosynthesis Estimates to Green Biomass

Regionally aggregated PSN_{net} estimates varied spatially in a similar pattern to scaled AGB (Fig. 5). As expected, the r -square of the relationships between scaled AGB and MODIS PSN_{net} was highest during peak greenness in 2001 and 2002. This finding was anticipated because, during peak greenness, the MODIS sensor receives relatively more vegetation signal than background.

Figure 5. Accumulated Moderate Resolution Imaging Spectroradiometer net photosynthesis (MODIS PSN_{net}) estimates for 2001 and 2002 compared with scaled aboveground green biomass from a similar period. For 2001, the composite periods of accumulation for MODIS PSN_{net} were from 1 to 137 for May, 1 to 161 for June, and 1 to 193 for July. For 2002, the periods of accumulation for MODIS PSN_{net} were for composite periods 1–145 for May, 1–161 for June, and 1–193 for July. 2001 scaled aboveground green biomass estimates were for 28 May, 15 June, and 15 July. 2002 scaled biomass estimates were for 22 May, 16 June, and 12 July. Note the aberrantly high productivity of Thiesson polygon 322 193. For all periods except July 2002, the sample size was 12. In July 2002, the sample size was 11 due to a small portion of missing imagery in the northeastern most Thiesson polygon.

The proportional increase in PSN_{net} was higher from June to July than was observed in AGB during the same time period. For example, in 2001, zone (Thiesson polygon) 320 209 exhibited a 2.2% increase in AGB but a 69% increase in PSN_{net} (Fig. 5). The disparity between observed AGB and PSN_{net} between these 2 periods might suggest that a potentially higher proportion of carbon was being allocated to roots or maintenance respiration, which is plausible because maintenance respiration is estimated as a function of air temperature in the algorithm (Running et al. 2000). This indicates that estimating biomass using MODIS productivity estimates will usually not be appropriate at the scales examined in this study because it is infeasible to quantify the root-to-shoot ratio, though estimates could be made (Scurlock et al. 2002) for entire regions of grassland vegetation. Despite this limitation, MODIS PSN_{net} estimates at regional scales can indicate spatial patterns that are not discern-

Table 3. Regional mean net primary productivity (NPP) and growing-season precipitation for the Little Missouri National Grasslands and adjacent area.

Variable	Year		
	2001	2002	2003
Precipitation (mm) ¹	383 (19) _a ² <i>n</i> = 12	291 (23) _b <i>n</i> = 12	235 (7) _b <i>n</i> = 12
NPP (kg·C·ha ⁻¹) ¹	3000 (42) _a <i>n</i> = 12	2437 (57) _b <i>n</i> = 12	2296 (34) _b <i>n</i> = 11

¹Values in parentheses are standard error of the mean (SEM).

²Means in the same row followed by the same subscript are not significantly different ($P \leq 0.05$).

able on the ground, thus bolstering the potential strength of 8-day summations of PSN_{net} as a monitoring tool. Another explanation for the dramatic increase in PSN_{net} is inflation of the FPAR response by the contamination of the LAI/FPAR signal by crops. Although the MODIS-derived PSN_{net} estimates were confined to represent only grassland pixels, it is likely that a number of these pixels contained mixtures of both grassland and crop vegetation. This is because fields of developed annual crops are intermingled with or adjacent to stands of senesced grass, thereby proportionally increasing the vegetation signal. In this situation, crops could possibly boost FPAR and therefore PSN_{net} , while the observed AGGB only represented grassland vegetation, thereby distorting the AGGB/ PSN_{net} relationship. In addition to crops, the inflated values of PSN_{net} could have also been due to woody vegetation influencing the spectral response of the satellites used in this study. However, as mentioned, we did mask out most of the woody vegetation, in addition to agricultural vegetation, using the mask provided by Jensen et al. (2001).

The relation between MODIS PSN_{net} and AGGB was stronger in 2001 than in 2002. In general, 2002 was drier and less productive than 2001, yielding a weaker FPAR signal due to partial obscuring by standing dead material from 2001. This was especially evident in May 2002, where no correlation was found between MODIS PSN_{net} estimates and scaled AGGB. In a similar study, Wylie et al. (1995) reported better relations between satellite data and biomass during favorable years ($r^2 = 0.8$ and 0.7) vs. nonfavorable years ($r^2 = 0.25$ and 0.67). The problem of obscurity presents a significant barrier to relating PSN_{net} estimates to AGGB in drier years. The response of MODIS PSN_{net} to precipitation fluctuations is evident when comparing the 2001 and 2002 growing seasons. For example, Thiesson polygon 322 193 (Fig. 5) exhibited aberrantly high biomass and commensurately high PSN_{net} during 2002 due to much higher than normal growing-season precipitation in the same polygon (Fig. 2).

Also, the current study area is relatively more homogeneous in terms of biomass and species life form composition than some regions analyzed in other similar studies, which related satellite data to observed biomass. For example, Prince and Tucker (1986) examined Advanced Very High Resolution Radiometer NDVI characteristics in very diverse grassland environments exhibiting 2–3-fold differences in end-of-season biomass. More restricted ranges of biomass (as in this study) will usually reduce the r -square statistic due to its sensitivity to the range of the independent variable (Wylie et al. 1995). However, if a broad range of biomass is examined, the relationship between NDVI and biomass will generally be greater.

For example, Wylie et al. (2002) related biomass to Thematic Mapper NDVI over a broad range of biomass and grassland types, resulting in very strong relationships ($r^2 = 0.85$). Using MODIS PSN_{net} estimates to compare with large differences in biomass will undoubtedly produce more favorable results when in contrast with regions of small differences in productivity.

Interannual NPP Trends

The analysis of variance of regional NPP for 2001–2003 revealed a highly significant ($P \leq 0.0001$) decreasing trend in productivity. Table 3 reveals that, estimated using MODIS NPP, 2001 was significantly ($P \leq 0.05$) more productive than either 2002 or 2003. Similarly, 2001 growing-season precipitation was significantly greater ($P \leq 0.05$) than either 2002 or 2003. These differences are clearly visible in the NPP images for the 3 years analyzed (Fig. 6).

Growing-season precipitation was high in 2001 (Fig. 2), while 2002 and 2003 were relatively dry, thereby providing ideal test beds to determine the usefulness of MODIS productivity products for assessing interannual differences in productivity. The similar trends between NPP and growing-season precipitation are important, as they indicate that MODIS can be used for regional grassland assessment, especially where objective coverage from a synoptic perspective is a priority. While the interannual NPP analysis is based on a large regional average (about 2 750 000 ha), the accuracy and precision of primary-productivity estimates at a particular point is, for some purposes, less useful than temporal trends of NPP (Zheng et al. 2003).

Possible Applications

The results presented here suggest that standard vegetation-productivity estimates derived from MODIS are suited for addressing regional, ecosystem, and global-level questions. Thus, users of these data must take care to ensure that the intended scale and scope for analysis realistically matches the information content of MODIS-derived vegetation productivity. For example, it would not be possible to evaluate the productivity of the grassland biome of North America using plot data, nor would it be wise to use 1-km² MODIS vegetation data for estimating the growth of vegetation on a small grazing allotment. The strengths of these coarse-resolution data are the regular, unbiased, and synoptic source of information they afford for evaluating vegetation productivity across broad geographic scales. To this end, aspects of forest plan revisions could be augmented using these data. Likewise, these data could be valuable for evaluating the productivity of large areas of grassland, such as in Mongolia. Another potentially appropriate use for MODIS vegetation data would be estimating carbon sequestration for all Conservation Reserve Program lands in the western United States.

CONCLUSIONS

The results of this study present a framework for linking small-scale field observations to improved MODIS PSN_{net} estimates while simultaneously providing needed insight to the response of MODIS productivity estimates to grassland biomass fluctuations. However, the large number of ground samples needed to calibrate

Figure 6. Mean and standard error of the mean (SEM) of net primary productivity (NPP) for the entire Little Missouri National Grasslands (LMNG) for 2001–2003. Only grassland pixels are represented. Polygons are Thiessen polygons around 12 weather stations. Dark gray line represents the administrative boundary of the LMNG.

the proposed scaling models still makes similar research a significant investment, especially when the goal is monitoring through time as opposed to a single point in the growing season. Despite this cost, with the exception of the ETM+ imagery, all data used to construct the model for both years of the study are freely available. Both ASTER and ETM+ provided sufficient spectral and spatial detail for constructing the scaling models at the spatial scale of Thiessen polygons used in this study (about 185 000 ha).

The relatively higher correlation between MODIS PSN_{net} and scaled AGGB in 2001 compared with 2002 indicates that years with beneficial growing conditions, and therefore higher biomass levels, provide more reliable results. In addition, monitoring should be conducted at peak greenness to enhance the probability of successful and accurate monitoring. Peak greenness could be estimated from temporal profiles of MODIS NDVI using the methods of White et al. (1997) or Zhang et al. (2003).

The similarity between precipitation and integrated MODIS PSN_{net} during peak greenness is encouraging and offers evidence that MODIS is a potentially valuable tool for evaluating moisture-driven grassland biomass fluctuations within a given year. Similarly, the interannual differences in NPP agreed with differences in growing-season precipitation in the same period. Despite demonstrating the utility of MODIS data for characterizing varying levels of grassland biomass, this study was limited in scope and applicability because it was restricted to northern mixed-grass prairie. If the study were designed to characterize relations across different expressions of grassland

vegetation (e.g., transition from shortgrass prairie to sagebrush-steppe communities), a broader range of vegetation productivity, and therefore MODIS-derived productivity estimates, would have been observed, making the findings more universally applicable. That said, MODIS estimates of vegetation productivity are freely available globally, which makes them an attractive tool for regionally monitoring grassland biomass fluctuations, especially in areas where ground data are limited.

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