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Phenology-assisted classification of C₃ and C₄ grasses in the U.S. Great Plains and their climate dependency with MODIS time series

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ARTICLE INFO

Article history:

Received 4 March 2012

Received in revised form 26 June 2013

Accepted 11 July 2013

Available online 15 August 2013

Keywords:

Great Plains

MODIS time series

Plant functional types

Phenology

Climate change

ABSTRACT

Grassland ecosystems in the North America are primarily composed of C₃ and C₄ plant functional types (PFTs) that have different responses to the changing climate. Knowledge of their spatial distributions and temporal variations helps us better understand the ecological functions and climate dependencies of grasslands. This study used the 500-m MODIS surface reflectance products (MOD09A1) from 2000 to 2009 to extract NDVI time series of C₃ and C₄ grass PFTs in different floristic regions (tallgrass, shortgrass, and mixed-grass prairies.) A set of phenology metrics, including *Start of Season*, *End of Season*, *Season Length*, *Peak NDVI*, *Peak Date*, and $\sum NDVI$, were found useful in delineating these grass types. A phenology-assisted decision tree classifier was developed to map the four grass PFTs in the Great Plains. The relative abundance of C₃ and C₄ PFTs generally showed the expected latitudinal shifts. Longitudinal shifts of tallgrass and shortgrass PFTs were also in agreement with the distributions of floristic prairie regions. In shortgrass and northern mixed prairies, shortgrass C₃ was located in the north while shortgrass C₄ was in the south. The native tallgrass C₄ remained in prairie remnants, although other native grasslands had been mostly converted to croplands or tallgrass C₃-dominated pastures. The inter-annual spatial variations of PFTs were statistically correlated with climate factors over a 10-year study period. The preliminary findings revealed that the strength and direction of correlations varied geographically and seasonally for different PFTs. This spatio-temporally explicit information may provide quantitative inputs in ecological forecasting for various climate change scenarios.

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1. Introduction

C₃ and C₄ grasses and cassulacean acid metabolism (CAM) plants are the three plant functional types (PFTs) that grow in temperate grassland ecosystems, although the CAM species are far less common in this region (Paruelo & Lauenroth, 1996; Risser, 1988; Teeri & Stowe, 1976). Generally, C₄ grasses grow in warmer environments, and C₃ grasses thrive in areas with lower temperature and greater water availability (Goodin & Henebry, 1997; Winslow, Hunt, & Piper, 2003). The higher water-use efficiency conferred by C₄ photosynthesis often sorts C₃ and C₄ grasses along precipitation gradients in a region, while other factors such as water availability, soil properties and terrain effects are also important constraints at local scales (Teeri & Stowe, 1976). Recent studies show that C₃ plants are likely to increase with elevated atmospheric CO₂ because of saturated C₄ photosynthesis at the current atmospheric concentrations (Morgan, Milchunas, LeCain, West, & Mosier, 2007).

However, warmer temperatures associated with global climate change may favor C₄ grasses (Collatz, Berry, & Clark, 1998; Ricotta, Reed, & Tieszen, 2004; Sage & Kubien, 2007). Natural and human disturbances such as fire, grazing, seeding and irrigation also directly affect the distribution of C₃ and C₄ grasses (Hunt et al., 2003). These shifts may affect ecosystem biogeochemical cycles in the long run, and therefore are important for ecosystem forecasting and improved global climate modeling (Collatz et al., 1998; Jung, Henkel, Herold, & Churkina, 2006; Potter, Klooster, Huete, & Genovese, 2007).

Intensive research has been conducted to investigate the physiological and ecological functions of the C₃/C₄ relative abundance in grasslands (e.g., Collatz et al., 1998; Epstein, Lauenroth, Burke, & Coffin, 1997; Sage & Kubien, 2007; Teeri & Stowe, 1976; Winslow et al., 2003). Most of these studies are initiated from historical records such as C₃/C₄ species richness and carbon isotope compositions at selected geographical locations. The modeled outputs at coarse, degree-grid units thus have large uncertainties in explaining climate controls of C₃/C₄ distributions and grassland ecosystem processes (Edwards & Still, 2008; von Fischer, Tieszen, & Schimel, 2008; Wan & Sage, 2001). Satellite remote sensing, owing to its global coverage and frequent observation capabilities, could provide spatially explicit information about C₃ and C₄ distributions and their temporal variations (Foody &

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Dash, 2007; Goodin & Henebry, 1997; Tieszen, Reed, Bliss, Wylie, & DeJong, 1997).

Remote sensing has been successfully applied to extract global land use and land cover patterns. The MODIS Land Cover Product (MOD12Q1) (Friedl et al., 2002, 2009), for example, is currently one of the most commonly adopted land cover data sets for global biogeochemical models (Jung et al., 2006; Potter et al., 2007). With monthly AVHRR Normalized Difference Vegetation Index (NDVI) products, the U.S. Geological Survey (USGS) developed the 1-km land cover database and identified 159 seasonal land cover classes in the conterminous United States (Loveland et al., 1995). Using satellite imagery at much finer resolutions, various nation-wide efforts have also been made to extract more specific land surface covers. For example, the U. S. Department of Agriculture (USDA) National Agricultural Statistics Service (NASS) uses medium-resolution satellite images to produce annual Cropland Data Layer (CDL) maps for various states (Boryan, Yang, Mueller, & Craig, 2011). Landsat imagery was also applied to develop the 2001 U.S. National Land Cover Database at 30-m resolution (Homer, Huang, Yang, Wylie, & Coan, 2004). However, these land cover products were not designed to delineate C₃ and C₄ grasses; due to their spectral similarity, these two grass PFTs are often grouped into categories of herbaceous lands (Running, Loveland, Pierce, Nemani, & Hunt, 1995).

The seasonality of the C₃ and C₄ grasses has been reported in remote sensing-based grassland mapping studies (Goodin & Henebry, 1997; Peterson, Price, & Martinko, 2002; Price, Guo, & Stiles, 2002). Growth of C₃ grasses starts early in the spring and may have a second growing peak when temperature cools down in the fall, while the growth of C₄ grasses starts later than C₃ and ends with the first frost (Balasko & Nelson, 2005; Wang, Fritsch, Stacey, & Yang, 2011). Tieszen et al. (1997) used seasonal NDVI time series to examine the spatio-temporal variability of C₃ and C₄ grasses in major subdivisions of grasslands in the Great Plains. With 10-day ground spectra in a growing season, Goodin and Henebry (1997) reported that the normalized integrated NDVI against growing degree days optimally revealed the relative C₃/C₄ abundance in a tallgrass prairie in Kansas. Foody and Dash (2007) found that the derivative of the season-long cumulative vegetation index linearly increased with C₃ abundance while the week of maximum vegetation index linearly increased with C₄. These phenological features were examined in Wang et al. (2011) and a decision tree was developed to classify C₄ grasses in the tallgrass prairie.

C₃ and C₄ grass PFTs grow in mixed composition in the Great Plains, and their relative abundance varies temporally depending on weather conditions each year. Satellite-assisted information about the inter-annual variation of all grass PFTs and their climate controls have not been adequately documented. This study aimed to develop a phenology-assisted decision tree approach in identifying C₃ and C₄ grasses with frequent satellite observations, and in examining the linkage between their spatio-temporal variations and climate dynamics. This information could improve ecological modeling in the changing climate in this important grassland region.

2. Materials and methods

2.1. Study area and focus sites

The U.S. Great Plains covers 10 states in the central United States, and is composed of three floristic prairie regions of tallgrass, mixed-grass and shortgrass prairies (USGS NPWRC, 2013). Precipitation and grass species composition vary longitudinally although they are strongly affected by local variations such as soil properties and terrain. Divided approximately at the 100th meridian, the east of the Great Plains is a primarily sub-humid tallgrass prairie that receives 500–750 mm of annual precipitation. The west is a shortgrass prairie in the semi-arid High Plains that receives 250–500 mm of annual precipitation (Risser, 1988). As shown in Fig. 1, areas in between are the vast landscape of

mixed-grass prairie in which lands in the north are more commonly named northern mixed prairie (Barber & Billings, 2000).

Distributions of C₃ and C₄ grass PFTs in the Great Plains differ somewhat from the floristic prairie regions defined above. The C₃ and C₄ composition varies with latitude, ranging from up to 80% C₄ cover in southern Texas to nearly pure C₃ plants in northern states (Tieszen et al., 1997). The distributions are also affected by human disturbances. Since European settlement in the early 1800 s, the prairies, especially the eastern tallgrass prairies, have been predominantly converted to croplands and pasturelands with introduced C₃ grass species (Risser, 1988). With different soil and climate characteristics in this vast land, the same PFT in different prairie regions may possess different biophysical and phenological properties. To refine PFT classification for the region, we re-grouped grass types into tallgrass C₃, tallgrass C₄, shortgrass C₃ and shortgrass C₄. Different from other PFTs which are comprised of mostly native species, tallgrass C₃ species, such as Kentucky bluegrass (*Poa pratensis*), orchardgrass (*Dactylus glomerata*) and tall fescue (*Festuca arundinacea*), were introduced to the pasturelands of the region (Balasko & Nelson, 2005).

To examine distributions of these grass PFTs and their climate dependencies in different floristic regions, five focus study sites (as marked in Fig. 1) in the U.S. Great Plains were selected in this study. Managed under various conservation efforts, these study sites were less disturbed and provided good representation of C₃ and C₄ PFTs in tallgrass, shortgrass, and northern mixed prairies.

2.1.1. The Flint Hills and the Tallgrass Prairie National Preserve, Kansas (Tallgrass C₄)

The Flint Hills in Kansas, with an area of 1.6 million ha, is the largest remnant of unplowed tallgrass prairie in the North America. C₄ grasses dominate the grassland. Common grass species are big bluestem (*Andropogon gerardii*), little bluestem (*Schizachryum scoparium*), Indiangrass (*Sorghastrum nutans*) and switchgrass (*Panicum virgatum*). C₃ grasses cover less than 20% of the grassland, mostly tall fescue in pasturelands and hayfields.

In the middle of the Flint Hills is the 4500 ha Tallgrass Prairie National Preserve (TPNP), which is managed by the National Park Service with a single conservation strategy (Wang et al., 2011). The TPNP served as a validation site in this study. In 2000–2001, a medium-resolution (30 m) land cover map of the TPNP was developed by the Kansas Geological Survey (Kindscher et al., 2011).

2.1.2. The Sand Hills, Nebraska (mixed C₃–C₄)

The Sand Hills grasslands are the largest unplowed remnant of mixed-grass prairie in the North America. They cover about 5 million ha in which dune formations dominate the landscape of the upland prairies. Most lands are privately owned and are used mainly for cattle grazing. The grasslands are dominated by a C₄ species community, but there is a rich mixture of C₃ and C₄ species in both tallgrass and shortgrass functional types (Schacht, Volesky, Bauer, Smart, & Mousel, 2000). Topographic position is an important factor in regulating PFT compositions. Tallgrass C₄ species such as little bluestem and sand bluestem (*Andropogon hallii*) often grow in sandy soils on dune tops and south-facing slopes. C₃ grasses such as needlegrass (*Stipa* spp.) and Kentucky bluegrass are more common on north-facing slopes and in interdunal valleys. The shallow-rooted shortgrass C₄ species, e.g. blue grama (*Bouteloua gracilis*), are also commonly observed in interdunal valleys (Barnes & Harrison, 1982).

2.1.3. The Central Plains Experimental Range, Colorado (shortgrass C₄)

The Central Plains Experimental Range (CPER) is a contiguous area of 6280 ha in north-central Colorado, operated by the USDA Agricultural Research Service. It is part of the Pawnee National Grassland, 78,100 ha of public land managed by the US Forest Service. The CPER is a typical shortgrass prairie dominated by shortgrass C₄ species such as blue grama. Shortgrass C₃ grasses are not common but can be

Fig. 1. The U.S. Great Plains and five study sites: (1) Flint Hills, Kansas; (2) Sand Hills, Nebraska; (3) Central Plains Experimental Range (CPER), Colorado; (4) Charles M. Russell National Wildlife Refuge (Russell Refuge), Montana; and (5) Cherokee Plain, Missouri. Also outlined are three floristic regions: shortgrass, tallgrass, and mixed-grass prairies. Adapted from the USGS Northern Prairie Wildlife Research Center.

observed along the valleys with finer-textured, high-moisture soils (Archer, 1984). At the coarse resolutions of satellite data used in this study, these local variations in grass species composition may not be identified.

2.1.4. The Charles M. Russell National Wildlife Refuge, Montana (shortgrass C_3)

The Charles M. Russell National Wildlife Refuge, hereafter referred to as the Russell Refuge, is a wildlife restoration habitat of 0.5 million ha extending along the Missouri River. Administrated by the U.S. Fish and Wildlife Service (USFWS), it is composed of a variety of badlands, river bottoms and forested coulees. Floristically this area belongs to the northern mixed prairie. A land cover map was developed by the USFWS Mountain-Prairie Region in 2001 (USFWS, 2012). Prairie grass types cover only a small proportion of this restored natural area. Typical shortgrass C_3 species, including needlegrass, wheatgrass (*Pascopyrum smithii*) and sagebrush (*Artemisia tridentata*), predominate in these prairie lands. In limited locations, shortgrass C_4 such as blue grama may be found. Only the prairie-land covers in the map were selected in this study.

2.1.5. The Cherokee Plain, Missouri (tallgrass C_4 remnants)

The Cherokee Plain has an area of 0.5 million ha in southwestern Missouri. More than 90% of the area has been converted to croplands and C_3 pastures. The remnant C_4 prairies are managed by state agencies and local conservation programs. Common C_4 grass species are similar to those in Flint Hills. The C_3/C_4 distributions at this site have been mapped and validated with a series of 15–30 m satellite images (Wang, Jamison, & Spicci, 2010) in a previous project by the Missouri Department of Conservation. At this site there were 10 prairie remnants, each with an area larger than 100 ha. These remnants served as the second validation source in this study.

2.2. Data sets

The 500-m, 8-day TERRA Moderate Resolution Imaging Spectroradiometer (MODIS) Surface Reflectance products (MOD09A1) from 2000 to 2009 were downloaded from the USGS Land Processes Distributed Active Archive Center. The US Great Plains could be fully covered by four MODIS tiles. With the red (R) and near infrared (NIR) spectral bands of the MODIS images, NDVI was calculated as $(NIR - R) /$

$(NIR + R)$ and was stacked into a 46-point time series for each year. In comparison with the 16-day or monthly MODIS NDVI/EVI products, the 8-day NDVI time series better showed phenological differences between C_3 and C_4 grasses, especially during the critical growth stages in early spring and late fall.

Only herbaceous lands in the Great Plains were examined in this study. The 2006 National Land Cover Database (NLCD) was used to pick up these lands (grassland/herbaceous, pasture/hay, barren land, and shrub/scrub). Other land covers such as annual crops, forests, wetlands, urban and water were masked out.

Monthly weather data from 2000 to 2009 were downloaded from the Parameter-elevation Regressions on Independent Slopes Model (PRISM) climate mapping system. The PRISM calculates spatially continuous weather data from station-level point records using parameter-elevation regressions with expert knowledge (Daly, Gibson, Taylor, Johnson, & Pasteris, 2002). The grid size was 2.4 arc minute (4 km). Two PRISM parameters, the monthly maximum temperature and monthly total precipitation, were used in this study to examine their relationships with grass cover variations over a 10-year period. Only data in the growing season (March–October) were analyzed. The pre-growth weather change may contribute to the relationship in March, while the impact to the second growth of tallgrass C_3 could be addressed in October (Wang et al., 2010). Data during grass senescence (November–February) were not used because they were not directly related to vegetation growth.

Training samples were extracted from the four study sites for classification in this study. The tallgrass C_4 samples were selected in the Flint Hills and Sand Hills. Different from the relatively homogeneous cover of the tallgrass C_4 in the Flint Hills, ground observations of pure tallgrass C_4 samples were not available in the mixed grasslands in the Sand Hills. Rather, indirect land cover information was collected from past studies. Tieszen et al. (1997) used soil data from the State Soil Geographic (STATSGO) database to map C_4 grass potentials for the Great Plains. Their results, validated with carbon isotopic data derived from native prairie sites (Mole, Joern, Oleary, & Madhavan, 1994), suggested that the southern Sand Hills was most favorable for the tallgrass C_4 growth. From their potential map, we extracted the tallgrass C_4 polygons with >80% cover in the southern Sand Hills. Training samples of the tallgrass C_4 were then randomly collected in these polygons. Shortgrass samples were from the CPER (shortgrass C_4) and the Russell Refuge (shortgrass C_3). To statistically examine phenology features of these grass types,

Fig. 2. A concept framework of the phenology-based decision tree. Phenology thresholds (listed in Table 1) for decision rules are displayed as bold.

we randomly extracted 688 points of tallgrass C₄ in the Flint Hills and Sand Hills, 330 points of shortgrass C₄ in the CPER and 334 points of shortgrass C₃ in the Russell Refuge. These training points were assumed pure samples of grass PFTs and the same data set was used in all years from 2000 to 2009. It should be noted, however, that uncertainties may be introduced because training samples were rarely pure in the 500-m MODIS images. The C₃/C₄ species mixture was commonly observed even in the well-maintained prairie remnants of the Great Plains.

2.3. Phenology-based decision tree

The MODIS NDVI time series were used to determine the phenological cycle from 2000 to 2009. Although the 8-day MODIS reflectance products have been processed using the maximum-value-composite (MVC) technique to reduce cloud effects (Huete et al., 2002), the produced NDVI trajectories were still jagged due to cloud residuals and temporal variation of atmospheric conditions. Points with heavily cloud-contaminated NDVI values were displayed as sharp spikes and were removed using a five-point median filter process (Wang et al., 2011). Then a second-order polynomial filtering approach (Savitzky & Golay, 1964) was applied to smooth out minor atmospheric effects. Quality control parameters of the MOD09A1 products were not used in this study because cloud noise could be fairly smoothed with these two filtering steps (Wang et al., 2011). Seasonality of grass PFTs was often asymmetric due to facts such as the second growth of tallgrass C₃ in the fall (Balasko & Nelson, 2005). Using NDVI time series with a relatively short interval (8 days), this study did not include further simulation such as the asymmetric Gaussian (Jönsson & Eklundh, 2004) or

logistic (Zhang et al., 2003) models. The smoothed data were directly processed for phenology analysis and decision-tree classification.

Based on continuous time series, a set of phenology metrics, e.g., the onset of greenness and season length, have been extracted in past studies (Jönsson & Eklundh, 2004; Tieszen et al., 1997; Zhang et al., 2003). In a previous study (Wang et al., 2011), these metrics were statistically examined to determine the optimal metrics in delineating warm-season and cool-season grasses in the tallgrass prairie. This study adopted a similar approach to extract phenology metrics in the Great Plains. With intensive sample points all over the study region, statistical analysis confirmed that the metrics in Wang et al. (2011) were also most useful among grass PFTs in this study. Additionally, the peak NDVI was introduced to reveal the apparent NDVI differences between shortgrass and tallgrass. The metrics used in this study included: 1) *Start of Season*: the date (day-of-year, or DOY) when NDVI increases to 20% of the amplitude; 2) *End of Season*: the date when NDVI decreases to 20% of the amplitude; 3) *Season Length*: the number of dates between *Start of Season* and *End of Season*; 4) *Peak NDVI*: the maximum NDVI value in a growing season; 5) *Peak Date*: the date that *peak NDVI* falls on; 6) *Accumulative NDVI* (ΣNDVI): the integral of NDVI between *Start of Season* and *End of Season*, which indicates biomass accumulation within each pixel.

Statistical properties of these phenology metrics were examined and a decision tree classifier was established to map the four grass types in the Great Plains. Fig. 2 outlines a concept framework of the decision tree. The phenology thresholds of decision rules were also marked in each branch. Tallgrass and shortgrass types can be easily delineated with **PeakNDVI_{tallgrass}** because tallgrass PFT had apparently higher values than shortgrass. A longer growing season and high NDVI values also contributed to the higher $\Sigma\text{NDVI}_{\text{tallgrass}}$ of tallgrass. For tallgrass

Table 1
Variables of phenology thresholds in the decision tree.

Thresholds	Year									
	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009
PeakNDVI_{tallgrass}	0.44	0.49	0.38	0.52	0.48	0.53	0.40	0.53	0.51	0.56
$\Sigma\text{NDVI}_{\text{tallgrass}}$	2.82	5.05	2.86	4.48	4.87	4.26	3.07	6.04	4.31	5.12
START_{tallgrass}^a	86	84	93	80	76	80	85	73	95	90
PeakDATE_{tallgrass}^a	143	137	138	141	148	142	133	150	160	167
LENGTH_{tallgrass}	227	271	256	258	276	253	244	265	232	226
START_{Lshortgrass}^a	88	92	105	100	96	93	59	68	88	115
START_{Rshortgrass}^a	120	184	151	104	113	115	101	101	134	113
PeakDATE_{shortgrass}^a	169	177	211	151	182	170	170	172	210	167

^a Units are in day of year (DOY).

PFTs, the tallgrass C_4 was characterized with a later *Start of Season* (**START_{tallgrass}**), later *Peak Date* (**PeakDATE_{tallgrass}**), and shorter *Season Length* (**LENGTH_{tallgrass}**) than the tallgrass C_3 . For shortgrass PFTs, the difference was less significant because the ranges of phenology metrics between the shortgrass C_3 and shortgrass C_4 were often overlaid on each other. In general, the shortgrass C_4 showed an earlier *Start of*

Season ($< \mathbf{START_L_{shortgrass}}$) than the shortgrass C_3 ($> \mathbf{START_R_{shortgrass}}$). In areas where the *Start of Season* fell in between, shortgrass C_4 could be delineated from shortgrass C_3 by a late *Peak Date* (**PeakDATE_{shortgrass}**).

Phenology thresholds of the decision rules were critical in the classification. With the rich set of training samples, the (mean $\pm$ standard deviation) was used as the envelope of the defined phenology threshold

Fig. 3. Latitudinal shifts of phenology metrics for (a) shortgrass prairie and (b) tallgrass/mixed-grass prairies in 2009. Each plot contains 100 samples along a north-south transect.

in each decision role, which led to about 80% accuracy at 95% confidence level ($\alpha = 0.05$). The thresholds may also be affected by temporal shifts of plant phenology in such a large geographical region. To examine these shifts, two north–south transects were randomly drawn in the west and the east of the Plains. The transect in the west was located in the northern mixed prairie and shortgrass steppe, while the one in the east passed through the mixed-grass and tallgrass prairies. The tallgrass prairie had been heavily converted to croplands as part of the Corn Belt and therefore, was not examined individually. A set of 100 grass points were randomly selected along each transect. To avoid mixed pixels, points close to non-grass types (on the NLCD land cover map) were not used. Using the 2009 image as an example, latitudinal variation of all six phenology metrics was examined. In the decision tree, the phenology thresholds having strong latitudinal dependency were adjusted by:

$$\text{Phenology metric} = \text{slope} * \text{latitude} + \text{intercept} \quad (1)$$

where slope represents the shift of a phenology metric per latitude degree.

With the decision tree in Fig. 2, the four types of grass PFTs were classified in the study region each year. Accuracy assessment was performed at two validation sites (the TPNP and Cherokee Plain) using published land cover maps from public sources and previous projects (Wang et al., 2011).

2.4. Correlation analysis

To examine the climate dependency of each grass PFT, in each study site a correlation analysis was performed between the 10-year percent covers of grass PFTs and monthly climate factors from March to October. A two-tailed student's t-test was used to test the significance of each correlation coefficient (degrees of freedom = 8). Only those correlations that were significant at a confidence level of 95% ($\alpha = 0.05$) were used to explore the climate control of grass PFTs in different floristic regions.

3. Results

3.1. Phenology thresholds from 2000 to 2009

The phenology thresholds in the decision tree showed apparent inter-annual variations (Table 1). For example, the *Peak NDVI* threshold between tallgrass and shortgrass PFTs was as low as 0.38 in 2002 and as high as 0.56 in 2009. The *Peak Date* threshold for the tallgrass C₄ was in mid May (DOY 133) in 2006 but was delayed about one month (DOY 167) in 2009.

Latitudinal shifts varied for phenology metrics in different floristic regions (Fig. 3). In the tallgrass/mixed-grass prairies, the *Peak Date* and *Start of Season* revealed positive slopes while the *End of Season* and *Season Length* had negative slopes, indicating that grasses at higher latitudes started growing later and ended earlier leading to a shorter growth cycle. As shown in Table 2, the delays were up to 3 days per

Fig. 4. Distributions of the four grass PFTs (with >50% occurrence from 2000 to 2009) in the U.S. Great Plains. The four study sites are also marked in the figure.

latitude degree, in agreement with the findings of Wang et al. (2011). The *Season Length* decreased 5 days per degree. In the shortgrass prairie, the latitudinal shifts were more heterogeneous. As shortgrass species are more sensitive to weather conditions than tallgrass species, local climate may have a stronger effect on phenology stage than latitudinal changes in this environment. The slopes for all phenology stages were significantly different from 0 in both floristic regions (Table 2). The coefficients of determination (R^2) in the shortgrass prairie, however, were low (0.11–0.32) and indicated weak latitudinal effects. With a student's t test, the *Peak NDVI* and $\sum NDVI$ did not show significant dependency on latitude in either region (Table 2). Corresponding to the phenology thresholds in Table 1, only $START_{tallgrass}$, $PeakDATE_{tallgrass}$, and $LENGTH_{tallgrass}$ were adjusted for their latitudinal shifts in the decision tree. The slopes and intercepts in Eq. (1) are listed in Table 2.

3.2. Distributions of grass PFTs

Grass in the Plains was distributed in mixed species composition and demonstrated considerable temporal variations from 2000 to 2009. The abundance of a grass type was represented by its occurrence frequencies in the 10-year period. For example, a pixel with >50% abundance of the tallgrass C₄ meant that it was classified as tallgrass C₄ in more than five of 10 years, which indicated the dominance of the tallgrass C₄ in this pixel. Fig. 4 displays the distributions of the four grass PFTs with >50% abundance in the Great Plains. Longitudinally it followed the general partition of floristic regions. Tallgrass PFTs (C₃ and C₄) grew in the east of the Great Plains while shortgrass PFTs (C₃ and C₄) were in the west. Latitudinally it agreed with the C₃/C₄ transitions as

Table 2

Latitudinal shifts of phenology metrics in tallgrass/mixed-grass prairies in the eastern plains and shortgrass prairie in the western plains.

	Tallgrass/mixed-grass				Shortgrass			
	Slope ^b	Intercept	R ²	t ^a	Slope	Intercept	R ²	t ^a
Peak NDVI	0.00	0.61	0.05	2.26	0.00	0.36	0.01	0.78
Peak date	2.95	61.48	0.33	6.88	−3.48	314.16	0.30	−6.72
Start of season	2.57	−3.36	0.52	10.46	−2.00	193.30	0.15	−4.15
End of season	−3.17	444.12	0.42	8.72	−6.00	514.74	0.32	−6.97
Season length	−5.75	447.48	0.53	−10.81	−4.00	321.44	0.11	−3.56
$\sum NDVI$	−0.03	9.39	0.01	−1.07	−0.04	3.95	0.02	−1.42

^a In the 100-sample student t test of the regression slope, the critical t at 99% confidence interval is 2.639.

^b Slope represents the shift of phenology metrics per latitude degree.

reported in past studies, i.e. shortgrass C_4 species were more dominant in the south while shortgrass C_3 species were mostly in the north. The latitudinal gradient of tallgrass PFTs, however, was less clear due to historical human interference that changed species composition. The tallgrass C_4 remained in prairie remnants such as those in Oklahoma, Kansas, and Nebraska. In areas of pasturelands, native C_4 prairie grasses were often converted to tallgrass C_3 species for high-quality forage in early spring and late fall (Risser, 1988).

The abundance distributions (0–100%) of the four grass PFTs better revealed their geographic patterns in the Great Plains (Fig. 5). As the largest remnant of tallgrass prairie, the Flint Hills was composed of almost pure tallgrass C_4 species (80–100% abundance). Similarly, the Sand Hills were characterized by >50% abundance of the tallgrass C_4 in mixture with shortgrass C_4 in this typically mixed-grass prairie land. The tallgrass C_3 was identified all over the eastern Great Plains, and was often in mixed distribution with tallgrass C_4 . The shortgrass steppe and northern mixed prairie held relatively homogeneous grass compositions. The high abundance of the shortgrass C_4 was common in southwestern Plains while the shortgrass C_3 was more common in the northwest.

The distribution patterns in Fig. 5 reflect the ecological control of floristic niches to grass PFTs. Table 3 summarizes the 10-year average cover of each grass PFT in the three floristic regions. Each value represents the average percent area in the floristic region from 2000 to 2009. In the tallgrass prairie, shortgrass PFTs were limited. Both tallgrass PFTs (C_3 and C_4) dominated while the tallgrass C_4 (17%) had slightly lower cover than the tallgrass C_3 (20%). The total amount of grassland in this region (37%) also confirmed that the tallgrass prairie had been heavily cultivated and converted to other lands. In the mixed-grass prairie, all grass PFTs grew while C_3 grasses covered more area than the C_4 grasses. Shortgrass C_4 (40%) and shortgrass C_3 (21%) predominantly occupied the shortgrass steppe.

3.3. Accuracy assessment

Due to limited availability of ground observations, it was difficult to perform year-to-year validation of the MODIS-derived grass PFT classifications in the Great Plains. We were able to collect ground reference data for the tallgrass C_4 at two validation sites using published sources and previous projects. The accuracies of shortgrass PFTs cannot be

Fig. 5. The 10-year abundance (0–100%) of the four PFT grass types: (a) tallgrass C_3 , (b) tallgrass C_4 , (c) shortgrass C_3 , and (d) shortgrass C_4 in the Great Plains.

Table 3

The 10-year average percent areas of the four grass PFTs in three floristic prairie regions (as marked in Fig. 1).

Percent area (%)			Floristic prairie regions		
			Tallgrass prairie	Mixed-grass prairie	Shortgrass prairie
Grass PFTs	C ₄	Tallgrass C ₄	16.91	11.75	6.80
		Shortgrass C ₄	0.07	9.93	39.94
	C ₃	Tallgrass C ₃	19.61	24.25	2.32
		Shortgrass C ₃	0.28	22.64	21.49
Total grass cover (%)			36.87	68.57	70.14

quantitatively assessed due to the lack of ground reference data in the study region.

3.3.1. Tallgrass Prairie National Preserve, Kansas

The TPNP in the Flint Hills was predominantly covered with unplowed native tallgrass C₄ species. In the 30-m land cover map developed by the Kansas Geological Survey (Fig. 6a), prairie grass covers 86% of the Preserve. Except in 2005, the 10-year grass distributions in this study displayed a consistent pattern of the tallgrass C₄ dominance in the TPNP (Fig. 6b). The abnormally high cover of tallgrass C₃ in 2005 may be related to arranged burning around the wayside exhibits that were installed in 2004 (NPS, 2005), which resulted in an earlier green-up feature in the following year. In other years, the tallgrass C₃ was in areas of cultivated land, which was a mixture of pastures, hayfields and annual crops. As the TPNP is a well-maintained conserved land of native tallgrass C₄ species, prairie grass cover of 86% in the land cover map was assumed constant from 2000 to 2009 in this validation site. The root-mean-square error (RMSE) of the MODIS-derived percent covers was 9.5% (Fig. 6c). When the results from 2005 were eliminated from the analysis, the RMSE reached 2.1% indicating that, in a relatively

homogenous tallgrass prairie land, this method could map the tallgrass C₄ with accuracies higher than 90%.

3.3.2. The Cherokee Plain, Missouri

At this validation site, smaller prairie remnants are managed in public lands. In a previous project, a medium-resolution class map was developed using ASTER satellite images in 2007 with an overall accuracy of 90% (Wang et al., 2010). Here, the MODIS-derived grass distribution in 2007 was compared with this published class map. Different from the TPNP, prairies in the Cherokee Plain were typically a mixture of tallgrass C₄ and C₃ species. In the 10 public prairie remnants with areas larger than 100 ha, the tallgrass C₄ and C₃ percent covers were compared between the MODIS-derived results in this study and the published land cover map (Fig. 7). Most points scattered along the 1:1 line. The largest discrepancy was observed in the Comstock Prairie (127 ha), Barton County. It was interpreted in Wang et al. (2010) that about half of this prairie was covered with the tallgrass C₄, while the other half was tallgrass C₃ pastures and annual crops. The mixed MODIS pixels of C₃ and annual crops resulted in similar phenology metrics as tallgrass C₄ and therefore, overestimated this grass type. Among the 10 prairie remnants, the RMSE of tallgrass C₄ percent cover was 20% and that of the C₃ was 24%. When both PFTs were considered, the RMSE reached 22% in delineating the tallgrass C₃ and C₄ in this mixed grassland.

3.4. Climate dependences of grass PFTs in the Great Plains

Climate patterns in the Great Plains varied spatially and temporally. Precipitation varied at different sites and revealed strong seasonal and inter-annual variations (Fig. 8a). Temperature in the Great Plains reached its highest values in July–August. Seasonal fluctuation patterns of monthly maximum temperature were similar in all study sites (Fig. 8b). Significant correlations between the 10-year percent covers

Fig. 6. The published and MODIS-extracted land cover maps in the TPNP: (a) the published 30-m land cover map; (b) MODIS-extracted grass covers from 2000 to 2009; and (c) comparison of the tallgrass C₄ percent covers between the two sources.

Fig. 7. Comparison of tallgrass C₃ and tallgrass C₄ percent covers in 10 prairie remnants in the Cherokee Plain, MO. The y-axis is the 2007 MODIS classification and the x-axis is the 2007 ASTER classification (from Wang et al., 2010). The two circled points represent the Comstock Prairie, Barton County.

of grass PFTs and the monthly climate factors are discussed for each study site, as follows.

3.4.1. Flint Hills, Kansas

The Flint Hills received the highest rainfall, most occurring in the spring and fall (Fig. 8a). The limited rainfall in summer resulted in an apparent summer trough. The site had much higher precipitation in 2005 and 2007. Spring temperature showed a more rapid increase than at the other sites (Fig. 8b). In 2007, temperatures in early spring were extremely high (20.4 °C in March). Agreeing with historical records, the Flint Hills grassland was predominantly covered with tallgrass C₄

Fig. 8. Variations of weather data from 2000 to 2009 at the four study sites: (a) monthly total precipitation, and (b) monthly maximum temperature. Only data from March–October are used.

species in the MODIS-derived maps (Fig. 9a). The second dominant PFT was tallgrass C₃ while shortgrass was limited.

Only tallgrass C₄ was examined in the correlation analysis at this site. Variation in precipitation did not strongly affect grass growth except in early spring and late summer. As shown in Table 4, tallgrass C₄ displayed a positive correlation with precipitation in March ($r = 0.76$) and negative correlation in August ($r = -0.72$). It is reasonable that higher precipitation in early spring accelerates the growth of the tallgrass C₄. In August, higher precipitation at the end of C₃ dormancy stage triggered its re-growth in fall (Balasko & Nelson, 2005; Wang et al., 2011) resulting in a reduced distribution of the tallgrass C₄. Temperature played a weaker role than precipitation in grass variations at this site. In March, the maximum temperature showed a weak, positive correlation with the tallgrass C₄ ($r = 0.56$) indicating that a warmer early spring also favored growth of C₄ species in this pure, tallgrass prairie. Correlation coefficients in other months were not significant.

3.4.2. Sand Hills, Nebraska

Along the longitudinal precipitation gradient, the Sand Hills received a higher amount of yearly rainfall than the shortgrass prairies in Colorado (CPER) and Montana (Russell Refuge). Both tallgrass and shortgrass PFTs grow in this typical mixed-grass prairie land. Based on soil properties, Tieszen et al. (1997) suggested that C₄ were dominant plant species in mild years. The derived abundance map in Fig. 4 agrees with their findings. The tallgrass C₄ dominated the land but was outcompeted by the shortgrass C₄ in the west of the site in certain years. For example, in 2009 tallgrass C₄ species covered 40% of the site, while shortgrass C₄ species reached 30% (Fig. 9b). The 10-year abundance map in Fig. 5 also reveals that tallgrass C₄ covered around 50–75% in the majority area of this site. Shortgrass C₄ species were clustered in the west end.

Both shortgrass and tallgrass C₄ PFTs were considered in the correlation analysis at this site (Table 4). Precipitation did not play a significant role with respect to any PFT. Tallgrass C₄ was negatively correlated with temperature in May–July with coefficients around -0.6 . In contrast, shortgrass C₄ was positively correlated with temperature in May ($r = 0.6$). These results indicate that a warmer climate in late spring-early summer suppresses the physiological development of the tallgrass C₄ and favors the shortgrass C₄ in this mixed-grass prairie.

3.4.3. Central Plains Experimental Range, Colorado

The CPER is in the semi-arid highlands and usually receives the least rainfall. It is a typical shortgrass prairie land dominated by shortgrass C₄ species (Fig. 9c). Tallgrass PFTs are rare at this site. As the CPER was a small site, three grassland-dominated counties (Weld, Logan and Morgan) nearby were used in the correlation analysis.

Only the shortgrass C₄ was analyzed at this site. The inter-annual variation in shortgrass C₄ abundance was negatively related to precipitation in April, May and July. However, increased precipitation in August strongly boosted its growth ($r = 0.75$). Grass variation at this site was not significantly sensitive to temperature.

3.4.4. Charles M. Russell National Wildlife Refuge, Montana

The Russell Refuge is located in the cold Montana upland prairie and its precipitation showed the largest inter-annual variations. Among the four sites, it received the second highest rainfall in 2001, 2005 and 2007, but suffered from droughts in other years. In agreement with published sources, the northern mixed prairie land at this site was predominantly covered by shortgrass C₃ species (Fig. 9d). Herbaceous prairie lands were limited in the Russell Refuge. For this reason, two prairie-dominated counties (Garfield and Prairie) along the Missouri River were selected for the correlation analysis.

Only the shortgrass C₃ was considered at this site. In this cold prairie land, grasses started their growth late and therefore, were not sensitive to weather variations in March–April (Table 4). Precipitation had a strong effect on grasses in summer and mid-fall. It was negatively related to the abundance of the shortgrass C₃ in July ($r = -0.58$) and positively

Fig. 9. The 2000–2009 percent areas of grass PFTs at the four sites: (a) Flint Hills, KS; (b) Sand Hills, NE; (c) CPER, CO; and (d) Russell Refuge, MT.

related in August and October ($r = 0.79$ and 0.73 , respectively). Temperature did not have a strong effect on the shortgrass C_3 until May ($r = -0.74$).

In Fig. 9c–d, the shortgrass C_3 is overestimated at the CPER site in 2000–2001, and the shortgrass C_4 is overestimated at the Russell Refuge site. Close examination of the MODIS time series in 2001 revealed that phenology differences in shortgrass C_3 and C_4 species were overturned in this year. In nine of the 10 years from 2000 to 2009, the shortgrass C_3 had earlier peak dates. In 2001, however, the shortgrass C_3 at the Russell Refuge had a later peak date than the shortgrass C_4 at CPER. The abnormally high precipitation in 2001 may have contributed to this phenomenon at both sites.

4. Discussion

Phenological differences in vegetation types can be detected from satellite time series along a growing season. In this study, these differences were applied in a knowledge-based decision tree to classify

grass PFTs in the Great Plains. The primary limitations to phenology-assisted classification were the inter-annual weather variations that directly affect the growth of grass PFTs in each year. The abrupt inter-annual variations in Table 1 reflected weather influences to grass PFTs in the study region. The inter-annual variations in phenology metrics were correlated with both temperature and precipitation, although the direction and strength of the correlations varied for different PFTs in different growing stages. Rare and extreme weather conditions can result in phenology differences between PFTs (e.g. shortgrass C_4 and shortgrass C_3 in 2001) that are opposite to those in regular years, resulting in considerable classification errors. Nevertheless, phenology metrics provided representative characteristics for each grass PFT. The decision tree used in this study could be a practical approach in large-area, long-term applications to determining grass PFTs.

Over the 10-year period from 2000 to 2009, classifications of grass PFTs in this study agreed with the floristic definitions long recognized by phytogeographers (e.g. Risser, 1988). The general latitudinal distributions of C_3 and C_4 PFTs identified in this study agreed with the

Table 4

Correlation coefficients between site-level grass covers and monthly climate factors in a 10-year analysis. Only coefficients that are statistically significant are listed (two-tailed t test, $df = 8$).

		March	April	May	June	July	Aug.	Sept.	Oct.
<i>Precipitation (monthly total)</i>									
Flint Hills	Tallgrass C_4	0.76					−0.72		
Sand Hills	Tallgrass C_4								
	Shortgrass C_4								
CPER	Shortgrass C_4		−0.68	−0.56		−0.59	0.75		
Russell Refuge	Shortgrass C_3					−0.58	0.79		0.73
<i>Temperature (monthly maximum)</i>									
Flint Hills	Tallgrass C_4	0.56							
Sand Hills	Tallgrass C_4			−0.62	−0.57	−0.58			
	Shortgrass C_4			0.60					
CPER	Shortgrass C_4								
Russell refuge	Shortgrass C_3			−0.74					

common understanding of C_4 and C_3 photosynthesis. Tallgrass and shortgrass PFTs separated longitudinally along the moisture gradient. These findings had general agreement with intensive studies in the past (e.g., Edwards & Still, 2008; Teeri & Stowe, 1976; Wan & Sage, 2001; Winslow et al., 2003). The climate dependences investigated in this study provided higher spatial details than in past studies. Seasonal weather variations from 2000 to 2009 had different effects on the annual distribution of PFTs in different floristic regions. Precipitation had a stronger and more significant effect on PFTs in all regions except the mixed-grass prairie (sampled at the Sand Hills). Precipitation in the early growing stages casts a positive effect on the tallgrass C_4 in the tallgrass prairie (sampled at the Flint Hills), while summer precipitation had a negative effect. In contrast, increased spring precipitation had a negative effect on the shortgrass C_4 in the shortgrass steppe (sampled at the CPER). Spring temperature played a significant role in all prairies except the shortgrass steppe. The correlation was positive for the tallgrass C_4 in the tallgrass prairie as well as for the shortgrass C_4 in the mixed-grass prairie. Increased spring temperature, however, had a negative effect on the tallgrass C_4 in the mixed-grass prairie and shortgrass C_3 in the northern mixed prairie (sampled at the Russell Refuge).

Although weather variations in the Great Plains did not show clear trends in the 10-year period, long-term warming and drought occurrences have become more frequent in past years. For a better understanding of ecological responses of the Great Plains to global climate change, primary PFTs in different floristic prairie regions should be examined specifically. In a scenario of warmer spring, tallgrass C_4 in the tallgrass prairie and shortgrass C_4 in the shortgrass steppe may increase. Tallgrass C_4 in the mixed-grass prairie, however, could be replaced by shortgrass C_4 . In a scenario of drier spring, tallgrass C_4 in the tallgrass prairie decreases, but shortgrass C_4 in the shortgrass steppe increases. However, these findings were preliminary because only 10-year data were examined in this study. Long-term climate data and satellite observations could support more detailed examination of climate dependency in this region.

The C_3 and C_4 species composition in the Great Plains is heterogeneous. Although the decision tree in this study was a binary classifier, the inter-annual differences in grass distributions classified from 2000 to 2009 (the abundance maps in Fig. 5) reasonably revealed the nature of C_3/C_4 mixed distribution in this region. Affected by weather conditions, grass abundance in a mixed pixel may vary year to year. Additionally, human disturbances served as an important force of inter-annual variations. Grazing, haying and various management policies may eventually change species composition in vast areas of rangelands. Furthermore, uncertainties in grass PFT classification may come from non-grass components in grasslands. For example, forbs in less maintained grasslands may green up earlier than the dominant C_4 grass species, which results in earlier *Start of Season* in this land. Shrubs may also delay the *End of Season* and extend the *Season Length*. In studies using fine-resolution data, these uncertainties could be further investigated to better understand the inter-annual variation in grass PFTs.

5. Conclusions

This study examined the use of phenological metrics extracted from the MODIS time series to delineate plant functional types (tallgrass C_4 , tallgrass C_3 , shortgrass C_3 , and shortgrass C_4) and to estimate their 10-year relative abundance in the U.S. Great Plains. Tallgrass C_4 mostly grew in the native remnants of tallgrass and mixed-grass prairies in the eastern Plains, shortgrass C_4 dominated the shortgrass steppe in the southwestern Plains, and shortgrass C_3 was more common at high latitudes in the northwest. The relative abundance of these PFTs was correlated with growing-season monthly precipitation and temperature over the past 10 years. The relationships varied geographically and seasonally, indicating different climate dependencies of these grass PFTs in the grassland ecosystems of the Great Plains.

Acknowledgment

The study was supported by the Director Innovation Foundation of the Center of Earth Observation and Digital Earth, Chinese Academy of Sciences (Grant No. Y2ZZ19101B) and the National Basic Research Program of China (973) (Grant No. 2009CB723906). We also thank Dr. Bruce K. Wylie at USGS EROS who kindly provided us the C_4 potential map in the Great Plains.

References

- Archer, S. (1984). The distribution of photosynthetic pathway types on a mixed-grass prairie hillside. *American Midland Naturalist*, 111, 138–142.
- Balasko, J. A., & Nelson, J. (2005). Grasses for northern areas. In R. F. Barnes, C. J. Nelson, M. Collins, & K. J. Moore (Eds.), (6th ed.) *Forages: An introduction to grassland agriculture*, vol. 1. Ames, Iowa: Blackwell Publishing.
- Barber, M. G., & Billings, W. D. (2000). *North American terrestrial vegetation* (2nd ed.). Cambridge: Cambridge University Press.
- Barnes, P. W., & Harrison, A. T. (1982). Species distributions and community organization in a Nebraska Sandhills mixed prairie as influenced by plant-soil-water relationships. *Oecologia*, 52, 192–202.
- Boryan, C., Yang, Z., Mueller, R., & Craig, M. (2011). Monitoring US agriculture: The US Department of Agriculture, National Agricultural Statistics Service, Cropland Data Layer Program. *Geocarto International*, 26(5), 341–358.
- Collatz, G. J., Berry, J. A., & Clark, J. S. (1998). Effects of climate and atmospheric CO_2 partial pressure on the global distribution of C_4 grasses: Present, past and future. *Oecologia*, 114, 441–454.
- Daly, C., Gibson, W. P., Taylor, G. H., Johnson, G. L., & Pasteris, P. (2002). A knowledge-based approach to the statistical mapping of climate. *Climate Research*, 22, 99–123.
- Edwards, E. J., & Still, C. J. (2008). Climate, phylogeny, and the ecological distribution of C_4 grasses. *Ecological Letters*, 11, 266–276.
- Epstein, H. E., Lauenroth, W. K., Burke, I. C., & Coffin, D. P. (1997). Productivity patterns of C_3 and C_4 functional types in the US Great Plains. *Ecology*, 78, 722–731.
- Foody, G. M., & Dash, J. (2007). Discriminating and mapping the C_3 and C_4 composition of grasslands in the northern Great Plains, USA. *Ecological Informatics*, 2, 89–93.
- Friedl, M. A., McIver, D. K., Hodges, J. C. F., Zhang, X. Y., Muchoney, D., Strahler, A. H., et al. (2002). Global land cover mapping from MODIS: Algorithms and early results. *Remote Sensing of Environment*, 83, 287–302.
- Friedl, M. A., Sulla-Menashe, D., Tan, B., Schneider, A., Ramankutty, N., Sibley, A., et al. (2009). MODIS collection 5 global land cover: Algorithm refinements and characterization of new datasets. *Remote Sensing of Environment*, 114, 168–182.
- Goodin, D. G., & Henebry, G. M. (1997). A technique for monitoring ecological disturbance in tallgrass prairie using seasonal NDVI trajectories and a discriminant function mixture model. *Remote Sensing of Environment*, 61, 270–278.
- Homer, C., Huang, C., Yang, L., Wylie, B., & Coan, M. (2004). Development of a 2001 National Landcover Database for the United States. *Photogrammetric Engineering and Remote Sensing*, 70, 829–840.
- Huete, A., Didan, K., Miura, T., Rodriguez, E. P., Gao, X., & Ferreira, L. G. (2002). Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sensing of Environment*, 83, 195–213.
- Hunt, E. R., Jr., Everitt, J. H., Ritchie, J. C., Moran, M. S., Booth, D. T., Anderson, G. L., et al. (2003). Applications and research using remote sensing for rangeland management. *Photogrammetric Engineering and Remote Sensing*, 69, 675–693.
- Jönsson, P., & Eklundh, L. (2004). TIMESAT – A program for analyzing time-series of satellite sensor data. *Computers and Geosciences*, 30, 833–845.
- Jung, M., Henkel, K., Herold, M., & Churkina, G. (2006). Exploiting synergies of global land cover products for carbon cycle modeling. *Remote Sensing of Environment*, 101, 534–553.
- Kindscher, K., Kilroy, H., Delisle, J., Long, Q., Loring, H., Dobbs, K., et al. (2011). Vegetation classification and mapping of Tallgrass Prairie National Preserve. *Natural Resource Report NRR/HTLN/NRR-2011/346* (<http://web.ku.edu/~kindscher/wp-content/uploads/2010/12/tallgrass1.pdf>, last accessed on Feb. 19, 2013).
- Loveland, T. R., Merchant, J. W., Brown, J. F., Ohlen, D. O., Reed, B. C., Olson, P., et al. (1995). Map supplement: Seasonal land-cover regions of the United States. *Annals of the Association of American Geographers*, 85, 339–355.
- Mole, S., Joern, A., O'Leary, M. H., & Madhavan, S. (1994). Spatial and temporal variation in carbon isotope discrimination in prairie graminoids. *Oecologia*, 97, 316–321.
- Morgan, J. A., Milchunas, D. G., LeCain, D. R., West, M., & Mosier, A. R. (2007). Carbon dioxide enrichment alters plant community structure and accelerates shrub growth in the shortgrass steppe. *Proceedings of the National Academy of Sciences*, 104, 14724–14729.
- National Park Service (2005). Tallgrass Prairie National Preserve: Long-range interpretive plan. http://www.nps.gov/history/history/online_books/tapri1/ip.pdf (last accessed on May 15, 2013).
- Paruelo, J. M., & Lauenroth, W. K. (1996). Relative abundance of plant functional types in grasslands and shrublands of North America. *Ecological Applications*, 6, 1212–1224.
- Peterson, D. L., Price, K. P., & Martinko, E. A. (2002). Discriminating between cool season and warm season grassland cover types in northeastern Kansas. *International Journal of Remote Sensing*, 23, 5015–5030.
- Potter, C., Klooster, S., Huete, A., & Genovesi, V. (2007). Terrestrial carbon sinks for the United States predicted from MODIS satellite data and ecosystem modeling. *Earth Interactions*, 11(13).
- Price, K. P., Guo, X., & Stiles, J. M. (2002). Optimal Landsat TM band combinations and vegetation indices for discrimination of six grassland types in eastern Kansas. *International Journal of Remote Sensing*, 23, 5031–5042.

- Ricotta, C., Reed, B. C., & Tieszen, L. T. (2004). The role of C₃ and C₄ grasses to interannual variability in remotely sensed ecosystem performance over the US Great Plains. *International Journal of Remote Sensing*, 24, 4421–4431.
- Risser, P. G. (1988). Diversity in and among grasslands. In E. O. Wilson (Ed.), *Biodiversity* (pp. 176–180). Washington D.C.: National Academy of Sciences.
- Running, S. W., Loveland, T. R., Pierce, L. L., Nemani, R. R., & Hunt, E. R. (1995). A remote sensing based vegetation classification logic for global land cover analysis. *Remote Sensing of Environment*, 51, 39–48.
- Sage, R. F., & Kubien, D. S. (2007). The temperature response of C₃ and C₄ photosynthesis. *Plant, Cell & Environment*, 30, 1086–1106.
- Savitzky, A., & Golay, M. J. E. (1964). Smoothing and differentiation of data by simplified least squares procedures. *Analytical Chemistry*, 36, 1627–1639.
- Schacht, W. H., Volesky, J. D., Bauer, B., Smart, A. J., & Mousel, E. M. (2000). Plant community patterns on upland prairie in the eastern Nebraska Sandhills. *The Prairie Naturalist*, 32, 43–58.
- Teeri, J. A., & Stowe, L. G. (1976). Climatic patterns and the distribution of C₄ grasses in North America. *Oecologia*, 23, 1–12.
- Tieszen, L. L., Reed, B. C., Bliss, N. B., Wylie, B. K., & DeJong, D. D. (1997). NDVI, C₃ and C₄ production and distributions in Great Plains grassland land cover classes. *Ecological Applications*, 7, 59–78.
- U.S. Fish and Wildlife Service (2012). *Comprehensive conservation plan: Charles M. Russell National Wildlife Refuge, UL Bend National Wildlife Refuge. Lakewood, CO: U.S. Department of the Interior, Fish and Wildlife Service, Mountain-Prairie Region.* (323 pp.).
- USGS Northern Prairie Wildlife Research Center (2013). Regional trends of biological resources – Grasslands: Prairie past and present. <http://www.npwrc.usgs.gov/resource/habitat/grlands/pastpres.htm> (last accessed on 02/25/2013).
- von Fischer, J. C., Tieszen, L. L., & Schimel, D. S. (2008). Climate controls on C₃ vs. C₄ productivity in North American Grasslands from carbon isotope composition of soil organic matter. *Global Change Biology*, 14, 1141–1155.
- Wan, C. S. M., & Sage, R. F. (2001). Climate and the distribution of C₄ grasses along the Atlantic and Pacific coasts of North America. *Canadian Journal of Botany*, 79, 474–486.
- Wang, C., Fritschi, F. B., Stacey, G., & Yang, Z. (2011). Phenology-based assessment of perennial energy crops in North American Tallgrass Prairie. *Annals of the Association of American Geographers*, 101, 741–751.
- Wang, C., Jamison, B., & Spicci, A. (2010). Trajectory-based warm season grass mapping in Missouri prairies with multi-temporal ASTER imagery. *Remote Sensing of Environment*, 114, 531–539.
- Winslow, J. C., Hunt, E. R., & Piper, S. C. (2003). The influence of seasonal water availability on global C₃ vs C₄ grassland biomass and its implications for climate change research. *Ecological modeling*, 163, 153–173.
- Zhang, X., Friedl, M. A., Schaaf, C. B., Strahler, A. H., Hodges, J. C. F., Gao, F., et al. (2003). Monitoring vegetation phenology using MODIS. *Remote Sensing of Environment*, 84, 471–475.