Soil Water and Temperature Explain Canopy Phenology and Onset of Spring in a Semiarid Steppe

Lynn M. Moore, William K. Lauenroth, David M. Bell, and Daniel R. Schlaepfer

ABSTRACT—It is well known that the timing of growth and development influences critical life stages of all organisms. The seasonal dynamics of ecosystems are usually well explained by photoperiod and temperature. However, phenological patterns in water-limited ecosystems are rarely studied and insufficiently explained by these two variables. We tested how onset (i.e., initiation of plant growth) and seasonality of plant growth are influenced by soil temperature and soil water. We collected seven years of daily measurements of near-surface reflected radiation, soil moisture, and soil temperature at an exclosure on the Shortgrass Steppe Long-Term Ecological Research Site, a semiarid ecosystem in the western Great Plains of the United States.

We determined that soil water content must be close to field capacity and soil temperature must be above 0°C to initiate a phenological response. We show for the first time that onset of spring and subsequent seasonal patterns of plant growth depend on both soil temperature and soil moisture. Our findings bear important implications for understanding responses of the shortgrass steppe and other semiarid ecosystems to climate change. Inadequate combinations of degree days and soil water may result from future precipitation and temperature, which are predicted to diverge from current patterns. Historical expectations about spring green-up, for example, for land and livestock management, seasonality of growth, and productivity, may fail and can only be replaced by taking both precipitation and temperature into account.

Key Words: accumulated soil water, growing degree day, onset of spring, phenology, shortgrass steppe

Introduction

The seasonal dynamics of growth and reproduction are of fundamental importance to ecosystem function. Phenology, the study of the timing of biological events, describes the intra-annual dynamics of ecosystems (Walther et al. 2002), providing observations that are particularly sensitive and simple indicators of climate change (Schwartz 1994; Cayan et al. 2001; Menzel 2003; Menzel et al. 2006; Schwartz et al. 2006). A large number of studies have found that air temperature is a primary driver of vegetation phenology (Zhang et al. 2004; Bertin 2008; Clark and Thompson 2010). This is true in ecosystems without chronic seasonal water stress; however, the effects of temperature on vegetation phenology may be critically modulated by soil water availability in arid and semiarid ecosystems (Dickinson and Dodd 1976; Sala et al. 1992; White et al. 1997).

The shortgrass steppe occupies the driest and warmest portion of the US Great Plains. The vegetation on the shortgrass steppe is dominated by C_4 perennial caespitose grasses, is adapted to periodic droughts, and evolved under a large-herbivore grazing regime (Milchunas et al. 1988, 2008). Primary production of the shortgrass steppe is positively related to precipitation (Lauenroth 1979; Lauenroth and Sala 1992). Precipitation, however, is not a direct resource for plants, because they use water accessed mostly from the soil. Available soil water itself is influenced by a combination of soil properties, precipitation, and evapotranspiration, which is strongly related to temperature, among other factors. Because vegetation of these semiarid systems are dominated by belowground constraints such as root competition for limited soil water and higher allocation to belowground biomass (Burke et al. 1998), soil temperature and soil water are the two most important factors that influence

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phenology. Consequently, understanding the phenology of arid and semiarid vegetation requires more difficult measurements in the soil instead of the standard meteorological observations of precipitation and air temperature, which suffice to explain phenological patterns in ecosystems without water stress. Several studies have examined the effects of precipitation on phenology and/or production and have found seasonality of precipitation can influence timing, production, and plant community composition in arid or semiarid systems (van Leeuwen et al. 2010; Villegas et al. 2010; Flanagan and Adkinson 2011; Prevéy and Seastedt 2014). However, to our knowledge, no study has investigated the within-year and among-year phenological patterns of a semiarid ecosystem using both soil temperature and soil water.

Climate change predictions for the shortgrass steppe include increases in temperature, more intense and longer summer droughts, a longer growing season, and a shift to more winter precipitation that will result in a net drying (IPCC et al. 2013; Maloney et al. 2014; Melillo et al. 2014). Drought in the Central Plains, which includes the shortgrass steppe, is predicted to have an 80% chance of developing into a megadrought in the coming decades (Cook et al. 2015). Under a changing climate, precipitation is predicted to be the most important environmental factor influencing phenological patterns in arid and semiarid systems (Badeck et al. 2004; Gordo and Sanz 2010: IPCC 2013). However, other models indicate that net primary production may increase in some Great Plains ecosystems due to fewer temperature constraints (Reeves et al. 2014). Extreme weather events are predicted to increase across the Central Plains with climate change (Melillo et al. 2014). Heavy rainfall events and longer dry intervals are associated with decreases in annual aboveground productivity across biomes including the shortgrass steppe (Heisler-White et al. 2009; Zhang et al. 2013). In any case, improved understanding of climate change consequences on phenological patterns will be important for land and livestock management, which depends on appropriate seasonal forage quantity and quality (Polley et al. 2013).

Current phenological research at the landscape scale utilizes vegetation indices derived from satellite data (de Beurs and Henebry 2005; Hudson Dunn and de Beurs 2011). Much of this research is focused on detecting change patterns and trends at regional or larger scales. However, near-surface-level studies are necessary to understand how vegetation responds at the plot scale to seasonal changes in soil water and soil temperature. Species-specific phenological studies are useful for pinpointing individual species patterns of growth and reproduction at the smallest plot scale (e.g., Schwartz et al. 2006; Dunnell and Travers 2011; Crimmins et al. 2011; CaraDonna et al. 2014). Most species-specific studies have proven less effective at capturing green-up events (but see Schwartz et al. 2006). In contrast, vegetation indices such as the normalized difference vegetation index (NDVI) have been used successfully at the near-surface scale to record changes in greenness (Aase et al. 1987; Goodin and Henebry 1997; Karnieli 2003; Przeszlowska et al. 2006). Kume and others (2011) determined that seasonal changes in the leaf area index (LAI) of a canopy could be estimated by transmitted near infrared and photosynthetically active radiation beneath a canopy measured at near-surface scale. NDVI derived from near-surface loses sensitivity at high LAI (>2), as is the case in ecosystems with moderate to dense canopies. However, in sparsely vegetated ecosystems (green leaf LAI between 0 and 2), NDVI reliably relates with canopy cover (Gamon et al. 1995). In the shortgrass steppe, green leaf LAI peaks at around 0.5 (Knight 1973), which makes this application of near-surface radiometry appropriate to quantify seasonal changes in greenness and to infer phenological patterns.

Using a seven-year record of near-surface reflected radiation, NDVI, soil moisture, and soil temperature observations from the Central Plains Experimental Range and from the Shortgrass Steppe Long-Term Ecological Research Site, we investigated how the timing of plant growth is influenced by soil temperature and soil water in a semiarid ecosystem. Specifically, we were interested in answering the following questions: (1) When do onset of growth and peak greenness occur? (2) How do soil temperature and water influence the timing of the onset of spring and the timing and value of NDVI at peak growth on the shortgrass steppe? (3) Do the relationships of soil temperature and soil water with phenological patterns vary across years with different climate conditions?

Methods

Study Site

The study site is located on the Central Plains Experimental Range (CPER) and Shortgrass Steppe Long-Term Ecological Research Site (SGS LTER) located 60 km east of Fort Collins CO (40°49′N, 104°46′W). The study was conducted within an exclosure located approximately

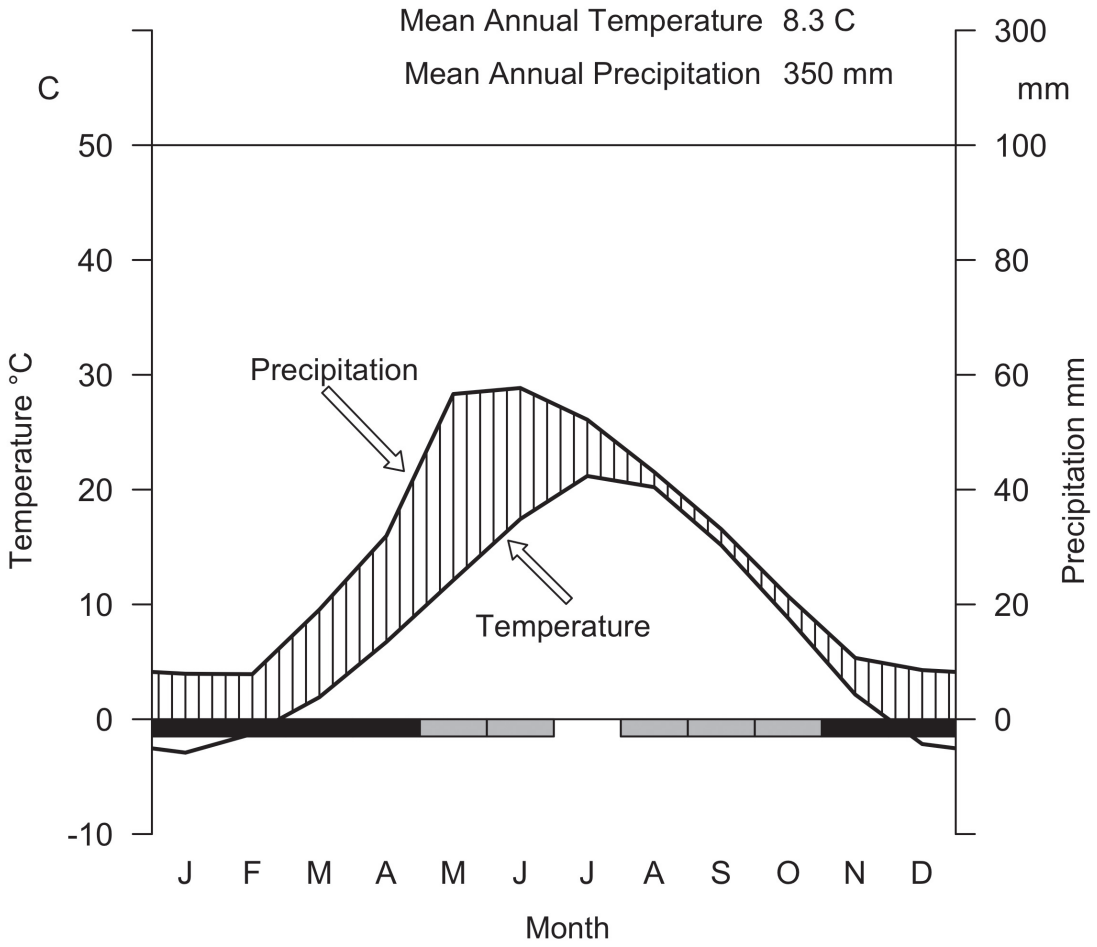

Figure 1. Climate diagram for the Shortgrass Steppe LTER (1939–2013), after Walter and Leith (1967). Lined areas indicate periods of relatively humid conditions. Black bars are months with frost, gray bars are months with a chance of frost; white bars are frost-free months.

2.4 km southwest of the CPER headquarters. An average annual precipitation of 350 mm and average annual temperature of 8.3°C characterize the climate as semiarid continental. Temperatures range from –11° to 29°C in winter and summer, respectively (Figure 1) (ARS-USDA 2014; Pielke and Doesken 2008). The majority of precipitation (70%) occurs as rain between April and September. Forty-eight percent of the average aboveground biomass consists of the dominant C_4 grasses blue grama (*Bouteloua gracilis* [H.B.K.] Lag.) and buffalograss (*Bouteloua dactyloides* [Nutt.] J. T. Columbus). Cool-season grasses contribute 8% of annual aboveground biomass and include an abundance of western wheatgrass *Pascopyrum smithii* (Rydb.) A. Löve. The remaining aboveground biomass is composed of forbs, shrubs, and cacti (Sims et al. 1978; Morgan et al. 2001).

Soil survey maps show the predominant soil type on the shortgrass steppe to be mollisols in the suborder ustoll (semiarid temperate) derived from parent materials consisting of Holocene alluvium and eolian materials from local sources (Kelly et al. 2008; NRCS-USDA 2015). Similar soil types characterize the northern third and east-central sections of the shortgrass steppe (Kelly et al. 2008). The shortgrass steppe soils show a great deal of variability, but they are also highly homogeneous because the two driving factors of shortgrass steppe soil development are a semiarid climate and a resilient plant community (Kelly et al. 2008).

For this study, we took advantage of long-term radiometer observations from 2002 to 2011 (see "Data" section for further details). This study was located on a single site within the CPER on the shortgrass steppe. The long time-series of radiometric observations provides a rare opportunity to examine phenological variation in

the same community across years with different temperature and precipitation pattern. It is also important to note the use of a single location in characterizing phenological variation contributes to limitations on inference. For example, we cannot account for spatial variation in soil characteristics, vegetation cover, or community composition in phenological patterns, all of which may cause variation in observed patterns (Cleland et al. 2006, 2007; Diez et al. 2012).

Because of the limitations of using a single location, and thus a single community, to quantify interannual variation in vegetation phenology, we examined the representativeness of radiometric results with individual-level phenological observations. To show that observations at this location are representative of other sites located on the CPER, we used species-specific phenological field observations from years 2002, 2003, 2005, 2006, 2007, 2010, and 2011 located 2.25 km southwest of the study site to verify phenological observations on a second location (details in the Appendix). We found a high positive correlation between the dates of the onset of spring derived from NDVI with phenological field observations of the first visible growth of 10 individual plants of blue grama and of western wheatgrass (Pearson correlation coefficient $r = 0.91$, $p < 0.01$; Appendix Figure S1). We also found a high positive correlation ($r = 0.81$, $p < 0.05$; Appendix Figure S2) between the date of peak greenness derived from NDVI for all seven years with the date when field observations indicated that the current-year growth of 10 individual plants of blue grama and of western wheatgrass individuals overtopped the previous year's standing dead biomass (see Appendix and Figs. S1 and S2). Given that these auxiliary data indicated that our radiometer was representative of general phenological patterns in the shortgrass steppe, that similar long-term data are rare, and that our main focus was on temporal patterns (i.e., interannual variation) and not spatial patterns, our approach, that of using data from a radiometer at a single location, is justified.

Data

In 2001 we installed a Skye 1800 two-channel radiometer (Channel 1 = red [R] 630 nm and Channel 2 = near-infrared [NIR] 862.5 nm, Skye Instruments, United Kingdom) in an ungrazed exclosure. We installed sensors 2.0 m aboveground with a viewing window equal to 1.66 m^2 ground area. A Campbell Scientific CR10X (Logan, Utah) data logger measured reflected radiation ($MJ/m^2/s$) every minute and averaged to hourly values. We calculated the normalized difference vegetation index (NDVI) from the noon-hour average of near-surface reflected radiation measurements: NDVI = [(NIR– R) / (R + NIR)] (Asrar et al. 1985; Huete et al. 1994; Reed et al. 1994; Sellers et al. 1994; White et al. 2009). We collected reflected radiation data in 2002, 2003, 2005, 2006, 2007, 2010, and 2011. Due to equipment malfunction, data for 2004, 2008, and 2009 were unavailable.

We collected climate data, including daily maximum and minimum soil temperature at 10 cm, measured manually using Campbell Scientific Model 107 (Logan, Utah) temperature probes. We measured daily precipitation at the CPER headquarters, located 2.4 km northeast, using a Campbell Scientific TE525 (Logan, Utah) tipping bucket rain gage. A Campbell Scientific CS615 (Logan, Utah) water content reflectometer measured soil water content onsite at three depths (0–10 cm, 10–20 cm, and 20–30 cm) within 1 m of the radiometer. Soil water content was collected hourly, averaged daily, and recorded as volumetric soil water content. We calibrated soil water content values from the reflectometer with onsite gravimetric soil water measurements at all three depths. In 2001 we collected six soil samples from 1 to 6 weeks apart from May 28 to August 31. We converted the resulting corrected volumetric water content to millimeters of water and analyzed it as total soil water content from 0 to 30 cm. Additionally, we used a pedotransfer function by Cosby et al. (1984) to calculate soil water potential from observed volumetric water content and soil texture.

The specific soil type at the study site is the Renohill-Shingle complex, 3% to 9% slopes derived from parent materials consisting of calcareous, clayey loamy residuum weathered from shale. This complex is well drained with a very low available water capacity of about 5 cm. The profile includes a surface layer of 0 to 10 cm of fine sandy loam, followed by 10 to 33 cm clay, 33 to 74 cm of clay loam, all on top of 74 to 84 cm of unweathered bedrock (NRCS-USDA 2015). We determined soil texture using the hydrometer method for eight samples within 1 m of the radiometer window to be sandy loam (76% sand, 9% clay, 15% silt). Soil textures on the CPER consist mostly of soils with a sand content of 35% to 70% (Burke and Lauenroth 1993). Fine-textured soils are more common elsewhere on the shortgrass steppe; therefore, extrapolating any results of this study to other locations on the shortgrass steppe should include specific consideration of soil texture differences (Burke and Lauenroth 1993).

Statistical Analyses

Using the delayed moving average approach (e.g., Reed et al. 1994; White et al. 1997; White et al. 2009), we estimated the date of onset of spring as the date when the smoothed five-day composite NDVI exceeded the dormant winter NDVI 10-day moving average and remained above it for the longest sustained increase in NDVI of the year. We determined the dormant winter mean by calculating the average NDVI between December 1 and March 1. We calculated accumulated soil growing degree-days by the BE method (Baskerville and Emin 1969) with a base temperature of 0°C (Goodin and Henebry 1998; Bartholomew and Williams 2005; McMaster 2005). We calculated available soil water days as follows:

Soil Water Day = 0, if Soil Water Content < Base
Soil Water Day = Soil Water Content – Base, if Soil Water Content > Base

We summed the available soil water days to generate our accumulated soil water variable. We estimated the base value in three steps for each year: (1) we took the average soil water content of the 10 days preceding the onset of spring as an initial estimate of the base value, (2) we calculated the soil water days using the estimated base value, and (3) we regressed the soil water days against NDVI. We found an optimal base value by inserting values higher and lower than the initial estimate until the best regression model fit was determined by significant ($p < 0.05$) R^2 values above 0.60. The soil water day base value signifies the minimum soil water content that is required to initiate a phenological response.

PHENOLOGY MODELS

To investigate relationships between NDVI, soil temperature, and soil water on the onset of spring and peak growth, we applied multiple regression models (e.g., Sparks et al. 2000; de Beurs and Henebry 2004, 2005; Sparks and Tryjanowski 2010). We regressed daily NDVI against all combinations of soil temperature, soil water, and coinciding quadratic and interaction terms for individual years and all years combined. Three models were examined: the soil-temperature-only model, which included an intercept, soil growing degree days, and the quadratic term; the soil-water-only model, which included an intercept, soil water days, and the quadratic term; and the full model (both soil temperature and soil water), which included an intercept, both quadratic terms, and the interaction between soil temperature and soil water. We used quadratic terms to represent the peaked nature of seasonal NDVI patterns. When both soil temperature and soil water were included, we incorporated an interaction. All quadratic and interaction terms used centered data to reduce collinearity.

We fit all variables using a linear mixed effects approach (Zuur et al. 2009; Pinheiro et al. 2013) with R package nlme version 3.1–113 (Pinheiro et al. 2013). The mixed effects approach allowed us to account for variation in daily NDVI responses among years by introducing random effects for the intercept, slope, quadratic, and interaction parameters. To account for temporal autocorrelation in the residuals, we incorporated an autoregressive covariance error structure. To test if the phenological dynamics differed from year to year, we fit soil water and soil temperature as fixed effects and year as a random effect using restricted maximum likelihood (REML) and examined the degree of interannual variation in the parameter estimates. Models that did not successfully converge were discarded. We compared models based on AIC (Akaike Information Criterion) and RMSE (Root Mean Square Error). Within a given model type (soil temperature only, soil water only, or full model), we performed model selection based on AIC for determining whether to incorporate random effects for each fixed effect in a given model. For example, with the soil-temperature-only model, we fit models with and without random effects for the intercept, the main effect of soil growing degree-days, and the quadratic effect of soil growing degree-days. We then compared the resulting eight soil-temperature-only models using AIC.

We determined peak NDVI as a function of soil temperature, soil water, or both by finding the maximum value of the best model for each variable. We calculated the coefficient of variation for the random effects (CV = [standard deviation for random effect] / [mean fixed effect]) to investigate how NDVI varies among years. We used the R statistical software to run all analyses (R Development Core Team 2013).

Results

Onset of Spring

In all years, the soil water base value, that is, soil water potential at the time of onset, was close to field capacity (–0.01 to –0.002 MPa; Table 1). The delayed moving average method estimated the onset of spring an average of 8 days earlier than species-specific field observations of blue grama and western wheatgrass for all years

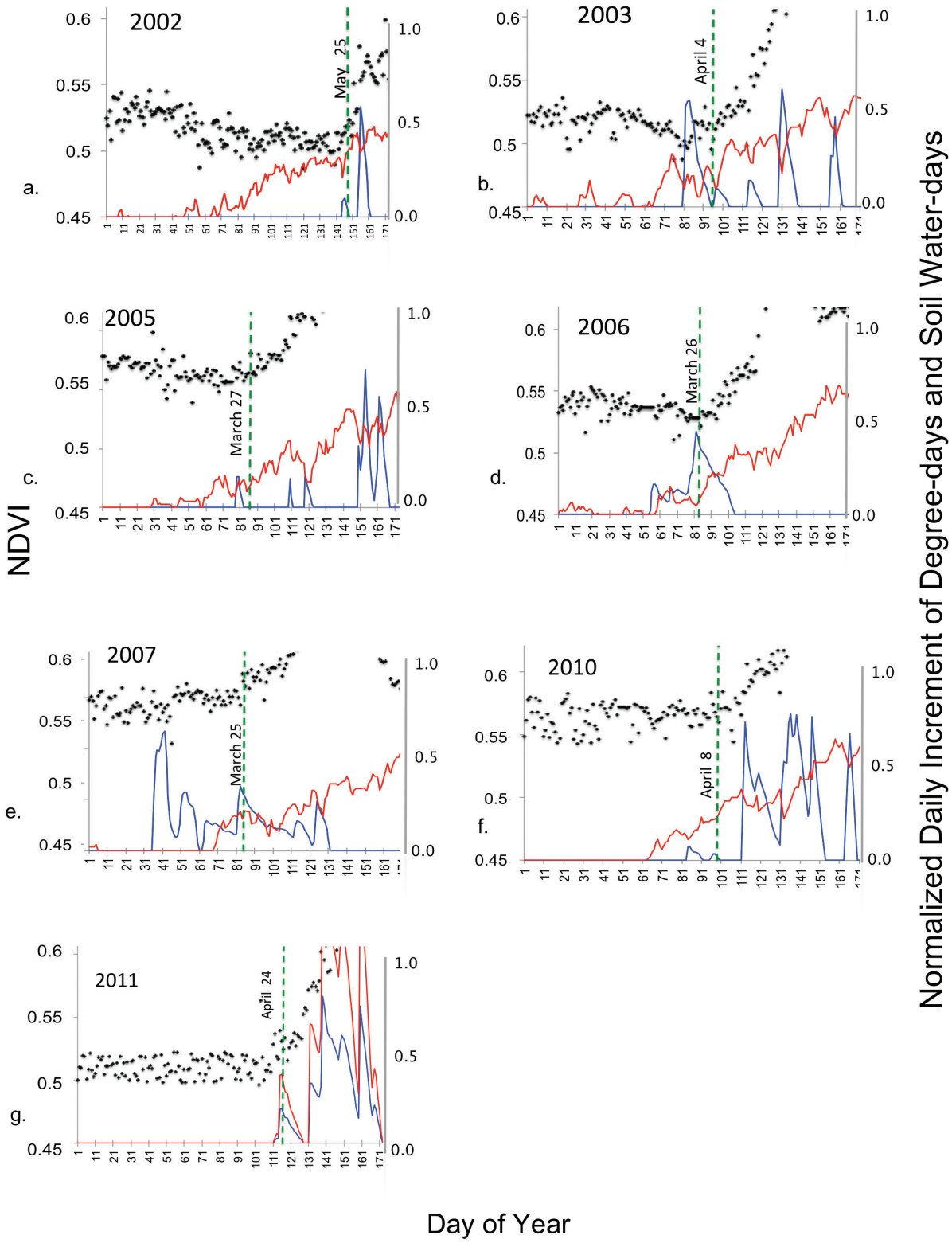

Figure 2. Onset of spring for observed NDVI vs. day of year for 2002, 2003, 2005, 2006, 2007, 2010, and 2011. Observed NDVI (black data points) plotted from January 1 to June 20 (left *y*-axis). Red line is the normalized daily increment of growing degree days in degrees Celsius (right *y*-axis). Blue line is the normalized daily increment of soil water days above the base value (i.e., wet day) (right *y*-axis). Date of onset denoted by green dashed line.

TABLE 1. Onset of spring dates and yearly moisture characteristics.

Year	PPT (mm)	SW (mm)	SW ψs (MPa)	Size (mm) (No. of events)	Onset date	Field date	Difference
2002	242	69	−0.0078	31.5 (2)	145	150	5
2003	322	87	−0.0030	11.9 (3)	94	105	11
2005	362	96	−0.0019	30.2 (3)	86	96	10
2006	300	95	−0.0020	30.7 (4)	85	103	18
2007	348	75	−0.0056	11.0 (1)	84	105	21
2010	360	84	−0.0034	21.8 (4)	99	106	7
2011	356	63	−0.0118	21.6 (7)	114	111	−3

Notes: PPT = annual precipitation. SW = soil water base value. SW ψs (MPa) = estimated soil matric potential for estimated onset date (Cosby et al. 1984). Size = amount of precipitation and, in parentheses, number of precipitation events associated with the number of wet days. Onset date = estimated day of year using delayed moving average (Reed et al. 1994). Field date = date of the average observation of first visible growth of blue grama and western wheatgrass. Difference = number of days between field and onset date (positive denotes field date is later in time, negative denotes field date occurred earlier).

(Table 1). The estimated dates of the onset of spring were significantly correlated to species-specific field observations ($r = 0.92$; $p < 0.001$) (See Appendix, Table S1, and Figure S1).

Effect of Soil Temperature and Moisture on the Onset of Spring

The soil growing degree days for all years associated with the onset varied between 94 and 779. The average amount of precipitation during 14 days prior to onset was 23.4 mm delivered in an average of 3.5 rainfall events (Table 1). In 2002 the onset of spring was on May 25, which is 27 to 61 days later than in the other six years. That year was the driest year since 1970 and one of the top 10 driest years in 73 years on the shortgrass steppe (ARS-USDA 2014). The NDVI for that year illustrated how growth was delayed until adequate moisture became available later in the growing season (Figure 2).

The field observations confirmed this delay (Table 1). In 2002 a soil water content of 69 mm, equivalent to $\psi s = -0.008$ MPa, was associated with the initiation of growth (Table 1). The degree-day requirement was met earlier, but no growth occurred until enough soil water became available on May 25 (Figure 2). In 2005 an above-average precipitation year, the onset of plant growth was March 27. The soil water content associated with the onset was 96 mm (equivalent to $\psi s = -0.002$ MPa) in 2005 (Table 1). The soil water content was high, yet the onset did not occur until sufficient heat energy had accumulated (Figure 2). In 2011 the spring was both dry and cold, and it was not until soil temperature rose above 0°C and water content approached field capacity (63 mm; equivalent to $\psi s = -0.01$ MPa) on April 24 that spring growth was initiated (Figure 2).

Effect of Soil Temperature on Peak NDVI

AIC indicated that models with yearly random effects for all parameters best explained the data. Model-predicted NDVI values compared poorly with observed NDVI. Particularly, larger NDVI values were underpredicted (Figure 3) from the onset of spring until sometime after peak NDVI had been reached (Figure 4). We found a significant correlation between predicted and measured date of peak NDVI, albeit with overprediction by 8 to 47 days ($r = 0.84$; $p = 0.01$). However, we found no significant correlation between predicted and measured values of NDVI on the day of the peak ($r = 0.65$; $p = 0.11$) (Table 2).

Effect of Soil Water on Peak NDVI

AIC indicated that models with yearly random effects for all parameters best explained the data. Model-predicted NDVI values compared poorly with observed NDVI. Particularly, medium NDVI values were under- and overpredicted (Figs. 3 and 4). We found a significant correlation between predicted and measured date of peak NDVI, albeit with under- and overprediction from 46 days earlier to 51 days later than measured date of peak NDVI ($r = 0.91$; $p < 0.01$). However, we found no significant correlation between predicted and measured values of NDVI on the day of the peak ($r = 0.53$; $p = 0.23$) (Table 2).

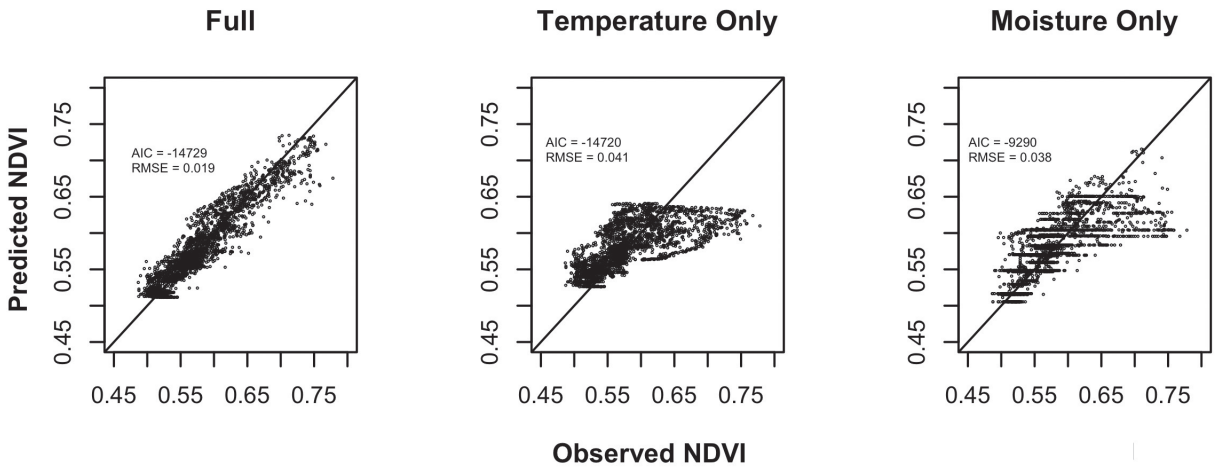

Figure 3. Predicted NDVI vs. observed NDVI for the soil-temperature-only model, soil-water-only model, and the full model, for seven years. AIC (Akaike Information Criterion) and RMSE (Root Mean Square Error) included.

TABLE 2. Dates of measured and estimated NDVI value of peak growth for each year.

Year	TEMP		SW		FULL		Measured NDVI	
	DOY	Value	DOY	Value	DOY	Value	DOY	Value
2002	202	0.6045	254	0.5701	197	0.5748	203	0.6407
2003	199	0.6206	134	0.6164	161	0.6885	169	0.7782
2005	199	0.6428	156	0.7156	168	0.7310	176	0.7552
2006	208	0.6275	270	0.6505	268	0.6990	265	0.7135
2007	196	0.6472	90	0.6440	132	0.6966	135	0.7426
2010	204	0.6371	138	0.6696	152	0.7345	172	0.7676
2011	212	0.6150	151	0.6780	165	0.6848	160	0.7490

Notes: TEMP = soil temperature only estimates; SW = soil water only estimates; FULL = soil temperature and soil water combined estimates; Measured NDVI = observed NDVI. DOY = numerical day of year. Value = NDVI value.

Combined Effects of Soil Temperature and Soil Water on Peak NDVI

AIC indicated that models with yearly random effects for all parameters best explained the data. Compared to the soil-temperature-only and soil-water-only models, the full model performed best in terms of AIC and RMSE (Figure 3). The predicted NDVI values for the full model resulted in a good fit when compared to the observed NDVI (Figure 3). We observed a significant negative fixed effect of the interaction effect (soil growing degree days · soil water days) (Appendix Table S2). Excluding the intercept, all regression parameters varied substantially from year to year for the full model (142% to 303%). We found a significant correlation between the model date of peak NDVI and the measured date of peak NDVI (r = 0.98; $p < 0.001$). Additionally, we found a correlation between the measured NDVI value and the full model NDVI value for peak growth (r = 0.86; $p < 0.05$). The full model tended to underpredict the NDVI value for peak growth, but it did a better job of predicting the date of peak NDVI than either the soil-temperature-only model or the soil-water-only model and identified areas where the NDVI responded to one variable more strongly than to the other (Figs. 3 and 4). In years that illustrate one major NDVI peak (2003, 2005, and 2010), the soil water coefficients are large and indicate that the NDVI is responding strongly to soil water inputs (Table 3, Figure 4). Soil temperature effects were negative across all years; however, the quadratic soil temperature term was small for 2003, 2005, and 2010, indicating soil temperature was less important later in the season. Partial autocorrelation function analysis indicated that a second-order autore-

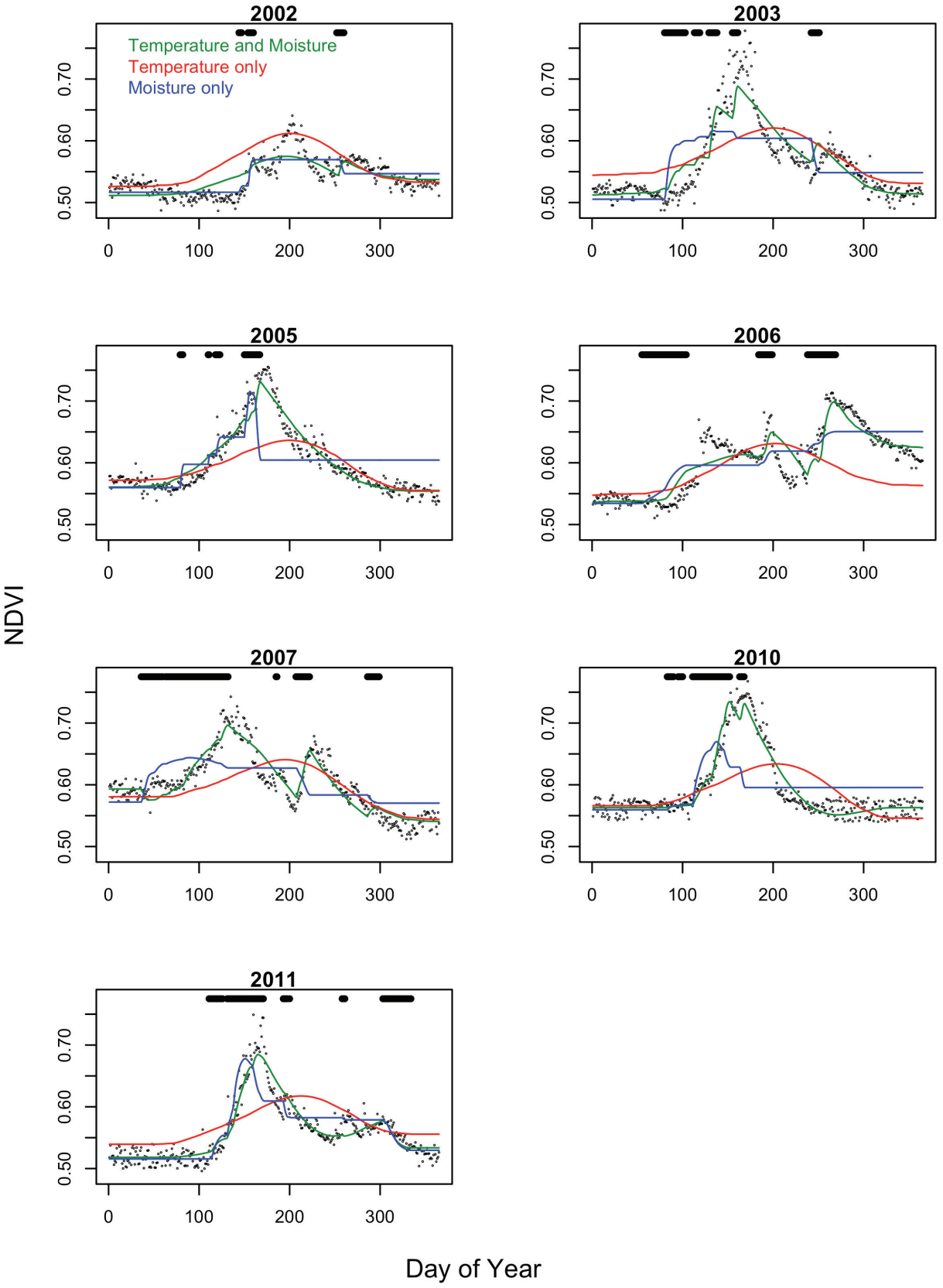

Figure 4. NDVI plotted over time (day of year) for the NDVI data (black data points), phenology models for soil temperature only (red), soil water only (blue), and the full model (green) for 7 years. Dotted line is onset of spring. Black bars along top show days when soil water content was above base value (minimum value of soil water required to initiate a phenological response).

TABLE 3. Coefficients of the full model for yearly regressions and combined average model.

Year	Intercept	ST	ST²	SW	SW²	ST · SW
2002	0.6171	0.4099	−0.2763	−1.0400	−3.4079	1.6211
2003	0.1110	−0.8463	0.2130	4.6707	13.4157	−5.0823
2005	0.5993	−1.4243	0.1816	3.5375	12.4482	−8.2720
2006	0.5793	−0.1211	−0.4664	0.3025	0.8939	−0.1685
2007	0.5938	−0.1219	0.0350	−0.0802	0.5322	−0.3884
2010	0.6153	−0.0940	0.5770	0.0709	1.3458	−2.2215
2011	0.5888	0.1735	0.7169	−0.1488	0.2539	−1.9401
AVG	0.5292	−0.2892	0.1401	1.0446	3.6403	−2.3502

ST = accumulated soil growing degree days, SW = accumulated soil water days, AVG = average model for all years.

gressive covariance error structure (AR2) was necessary to account for temporal autocorrelation. The estimated autocorrelations were 0.54 and 0.28 for the first- and second-order autoregressive terms.

Discussion

Our study successfully determined the date of the onset of spring, confirmed that soil temperature and soil water together influence onset of spring and peak growth, and demonstrated how variation of soil temperature and soil water among years influences the seasonal pattern of the shortgrass steppe. The importance of water in assessing phenology has previously been established, although most of the research has focused on short-term studies, on other measures of phenology, such as satellite-derived indices and flowering phenology, or on other ecosystems, such as warm deserts and Mediterranean climates (White et al. 1997; Peñuelas et al. 2004; Lesica and Kittelson 2010; Steinaker et al. 2010; Crimmins et al. 2011). To our knowledge, this is the first time the importance of including soil water in addition to soil temperature as an explanatory variable for vegetative phenology in a temperate semiarid ecosystem has been demonstrated.

Onset of Spring

The remote sensing community has developed several methods for extracting a spring onset date using satellite-derived vegetation indices. Problems with clouds, frequency, and scale are common with satellite observations, but these are not significant when using near-surface radiometric observations (Gamon et al. 1995; Kume et al. 2011). We define the onset of spring as the day of year when the NDVI values increased above the dormant winter NDVI mean (delayed moving average). An earlier assessment of methods using satellite data compared to field observations for North America found the delayed moving average method estimated the onset in northeastern Colorado approximately 10 days earlier than species-specific field observations (White et al. 2009). Our results are consistent with this study, as our NDVI estimates of onset averaged 8 days earlier than field observations. The discrepancy may be due to an increased sensitivity of the radiometer in picking up changes in greenness compared to visual-based observations, which examine individual leaves.

Effect of Temperature and Moisture on the Onset of Spring

Growing degree days are frequently used in agriculture because they predict well specific life stages of a particular crop using only easily available meteorological data (e.g., corn maturity) (Gilmore and Rogers 1958). For instance, Frank and Hoffman (1989) used growing degree days to predict forage production in rangelands when annual precipitation was above average. Such predictions assume that sufficient soil water is present, which it often is in an agricultural setting.

Our study demonstrated that the start of the growing season in a semiarid steppe is driven by soil temperature and soil water. A baseline study on the shortgrass steppe showed that species-specific flowering phenology was related to moisture availability (Dickinson and Dodd 1976). A similar species-specific study showed that soil

moisture in addition to cumulative air temperature explained a delay in onset of spring for two grass species in a semiarid grassland in China (Yuan et al. 2007). Our results support the results of these previous studies but differ significantly because we consider phenology at a scale larger than a single species. Our study showed that in all years, onset occurred close to or shortly after the first accumulation of soil water above the base value, stressing the importance of a critical accumulation of water as well as heat energy to initiate spring growth. This is consistent with studies that have found delays in leaf unfolding in Mediterranean shrubs (Peñuelas et al. 2004) and first flowering in southwestern US sky islands in direct response to dry conditions (Crimmins et al. 2011). Other studies indicate that dry conditions also may result in indirect effects on phenological patters. Lesica and Kittelson (2010), for instance, found that first flowering in a montane semiarid grassland advanced (occurred earlier) with less winter precipitation due to earlier snowmelt and soil warming. Similarly, drought advanced the onset of spring in a Mediterranean shrubland due to increased early-season temperatures caused by decreased latent heat exchange in a drier system (Bernal et al. 2011). Our results suggest that a dry year such as 2002 may delay initiation of growth and that extreme weather may impact the seasonal dynamics of the shortgrass steppe vegetation and likely of other semiarid ecosystems.

Effects of Soil Temperature and Soil Water on Peak NDVI

Our multiple regression mixed-effects model clearly demonstrated that a model including both soil temperature and soil water is necessary to explain the seasonal dynamics of NDVI on the shortgrass steppe. The shortgrass steppe often reaches a seasonal maximum of photosynthetic activity and growth rates during May and June, coinciding with longer days, optimal temperature, and increased precipitation (Menke and Trlica 1981; LeCain et al. 2002). In years with one major NDVI peak, the soil water coefficients are large and indicate that the NDVI is responding strongly to soil water inputs, especially during the early part of the season. Soil temperature effects were important early in the season but became less important later in the season because average temperature fluctuates much less from year to year than precipitation events. This suggests that as soil water inputs decrease, the increasing accumulated degree days are associated with drying soils and are likely influencing the decrease in the NDVI at the end of the growing season.

The shortgrass steppe is a pulse-driven system (Lauenroth and Sala 1992; Heisler-White et al. 2008; Lauenroth et al. 2014). Multiple peaks of photosynthetic activity and growth can occur during a single season (LeCain et al. 2002). A pattern of pulses in phenological activity is apparent when we consider the multimodal years 2006, 2007, and to a lesser degree 2011. In 2006 there were three peaks of growth and our model picked up the last two peaks. In 2007 our model predicted multiple growth peaks. Two peaks were identified in 2011, one strong early peak and a second weaker peak occurring in the fall. The highest value of NDVI for 2006 occurred on September 22; our model successfully captured this peak. Corroboration of this late peak was found with our species-specific field observations, which verified a green-up of blue grama during this month in 2006. The late fall moisture remained in the soil and likely influenced the relatively early onset of spring in 2007. A second strongly bimodal pattern in 2007 illustrated a second peak occurring on August 15; this too was verified by species-specific field observations. The soil-temperature-only or soil-water-only models were unable to capture these multiple peaks. The seasonal dynamic of NDVI, particularly with multiple peaks, was thus clearly responding to accumulation of soil water during the growing season when soil temperatures can be expected to be sufficient.

Caveats

While our use of a single radiometer constrains our realm of inference concerning the joint limitation of temperature and moisture on shortgrass steppe vegetation phenology, the idea of this joint limitation is consistent with the vast majority of shortgrass steppe responses to the abiotic environment (Lauenroth and Burke 2008). The shortgrass steppe ecosystem exhibits high degrees of spatial and temporal variation in ecosystem processes, including productivity (Lauenroth et al. 2008) and in physical characteristics such as soil texture (Burke and Lauenroth 1993). Due to this spatial variation, our results are not representative of the entire ecosystem. While we could not directly test the generality of our results, comparisons of NDVI with species-specific phenological data from another site in the area indicated general agreement. Furthermore, general soil

water dynamics at our site should be similar to other sites in the Great Plains that have comparable soils, dryness, and seasonality (Burke and Lauenroth 1993; Lauenroth et al. 2014). This is partly because overall characteristics of the soil at our site—well-drained, high sand content, and with a low available water capacity—occur frequently throughout the shortgrass steppe and in many other semiarid areas. However, additional work is needed to understand the degree to which the phenological patterns observed in this study vary spatially within the shortgrass steppe landscape.

Conclusions

The use of near-surface derived NDVI provides an important tool to link phenological responses with climate variables. Most species-specific or manual field observations do not record responses on a daily time step, and if so, not on a long-term basis, making it difficult to link the daily changes in soil water and temperature with daily changes in plant responses. Our study demonstrates the suitability of near-surface radiometric methods for long-term phenological studies, which account for annual variability and overall trends that may be occurring in response to a changing climate. This method is particularly well suited in systems with low plant cover such as arid and semiarid ecosystems to accurately measure how the timing of production responds to changing precipitation and temperature variables.

A large body of phenological research across temperate biomes has established that phenological responses are linked to temperature. In arid and semiarid ecosystems, the relationship between phenology and the environment is more complex. These water-limited, often pulse-driven systems are unable to respond to temperature as a single environmental cue; water must be part of the process. This has implications for understanding how climate change may influence the start and peak(s) of the growing season in semiarid grasslands. Ecosystems with increased spring temperature variability, for instance, advance spring onset less than ecosystems with less variable spring temperatures (Wang et al. 2014). This suggests that controls over phenology will be expressed through local abiotic variables, which in the case of the shortgrass steppe is water availability. Soils in the shortgrass steppe are mostly dry during the cold season because October to March receives little precipitation on average (Figure 1). The probability of precipitation events, however, is higher early in the growing season than during the rest of the growing season (Sala et al. 1992). Spring green-up on the shortgrass steppe thus relies on this specific pattern of precipitation seasonality for sufficient wetting of soils to initiate growth.

Despite the variability in spring temperatures, an advance of four to eight days in spring onset between 1900 and 2010 has been detected using phenological models in parts of the northern Great Plains and the western United States (Schwartz et al. 2012). However, an earlier study using satellite-derived NDVI found no trend in the timing of green-up on the western Great Plains from 1982 to 2006 (White et al. 2009). Flowering phenology patterns have shown the advance of first flowering day in the northern Great Plains of North Dakota (Dunnel and Travers 2011), in the Rocky Mountains of Colorado (CaraDonna et al. 2014), and in Montana (Lesica and Kittelson 2010).

Long-term effects of changing temperature and soil moisture may influence not only seasonal patterns and productivity but also the distribution of dominant grass species in both tallgrass and shortgrass ecosystems. Water stress has a negative effect on the reproductive phenology and productivity of, for instance, peripheral (edge) populations of blue grama on the shortgrass steppe and tallgrass prairie (Giuliani et al. 2013). Giuliana et al. (2013) found differential responses such that peripheral populations of blue grama flowered later when a mesic biome becomes arid and aboveground productivity was affected more when a dry biome becomes more mesic. Our study suggests that the seasonal timing of green-up and peak growth may respond negatively to overall increase in precipitation variability, to more years with droughts, and to a shift of spring precipitation to later in the season.

Given predictions that drought conditions combined with warmer temperatures will increase on the Great Plains in response to climate change (IPCC 2013; Maloney et al. 2014; Melillo et al. 2014; Cook et al. 2015), it is crucial for livestock and wildlife management that we understand how productivity in water-limited systems may respond. A recent study concluded that forecasted warming in semiarid grasslands would likely affect the aboveground productivity in these grasslands (Mowll et al. 2015). However, predicting the effects of warming will be difficult because the effects can vary from positive to negative and are influenced by community composition (Mowll et al. 2015). Changes in community composition are possible as a response to changes in seasonality of precipitation. For instance, altered seasonality of pre-

cipitation in a semiarid northern mixed-grass prairie in Colorado resulted in changes in cover and advanced flowering and senescence of exotic species (Prevéy and Seastedt 2014). Current research suggests a decrease in productivity due to both warming temperatures and increase in frequency of extreme weather events (Heisler-White et al. 2009; Zhang et al. 2013). The timing of forage production, as well as quantity and quality, is important for both wildlife and livestock management. Understanding how the timing, quantity, and quality of forage respond to changes in temperature and soil water availability is an area of research that could benefit from implementing surface radiometric techniques. We have shown that surface radiometry offers an excellent tool to track ecosystem response to climate change.

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Appendix

The majority of phenological research is focused on traditional methods of stage-based field observations or remote-sensing-derived vegetation indices. We used nearby species-specific phenological field observations to demonstrate a relationship between the near-surface radiometer-derived normalized difference vegetation index (NDVI), the date of onset of spring, and peak growth. We compared the estimated onset of spring date to phenological field observations of the dominant warm-season grass, blue grama (*Bouteloua gracilis* [H.B.K.] Lag.), and the dominant cool-season grass, western wheatgrass *Pascopyrum smithii* (Rydb.) A. Löve, specifically the average dates when the first visible growth occurred. We compared the date of peak NDVI for all seven years to phenological field observations of the dominant warm-season grass, blue grama, and the dominant cool-season grass, western wheatgrass, specifically the date when current-year growth overtopped the previous year's standing dead. Table S1 lists the day of year of onset of spring and peak growth for the measured NDVI and the average of blue grama and western wheatgrass. Figures S2 and S3 show the relationships between the dates of the radiometer measurements and the species-specific observations. These relationships show that the radiometers are indeed recording the same phenological events that are occurring elsewhere on the shortgrass steppe.

TABLE S1. Day of year (DOY) of onset of spring and peak NDVI and field observations, specifically the date when first visible growth occurred (onset) and the date when current year growth overtopped the previous year's standing dead (peak) for the average of blue grama and western wheatgrass.

Year	DOY onset measured NDVI	DOY onset average	DOY peak measured NDVI	DOY peak average
2002	145	150	203	232
2003	94	105	169	174
2005	86	103	176	188
2006	85	103	268	228
2007	84	105	135	165
2010	99	106	172	173
2011	114	111	160	195

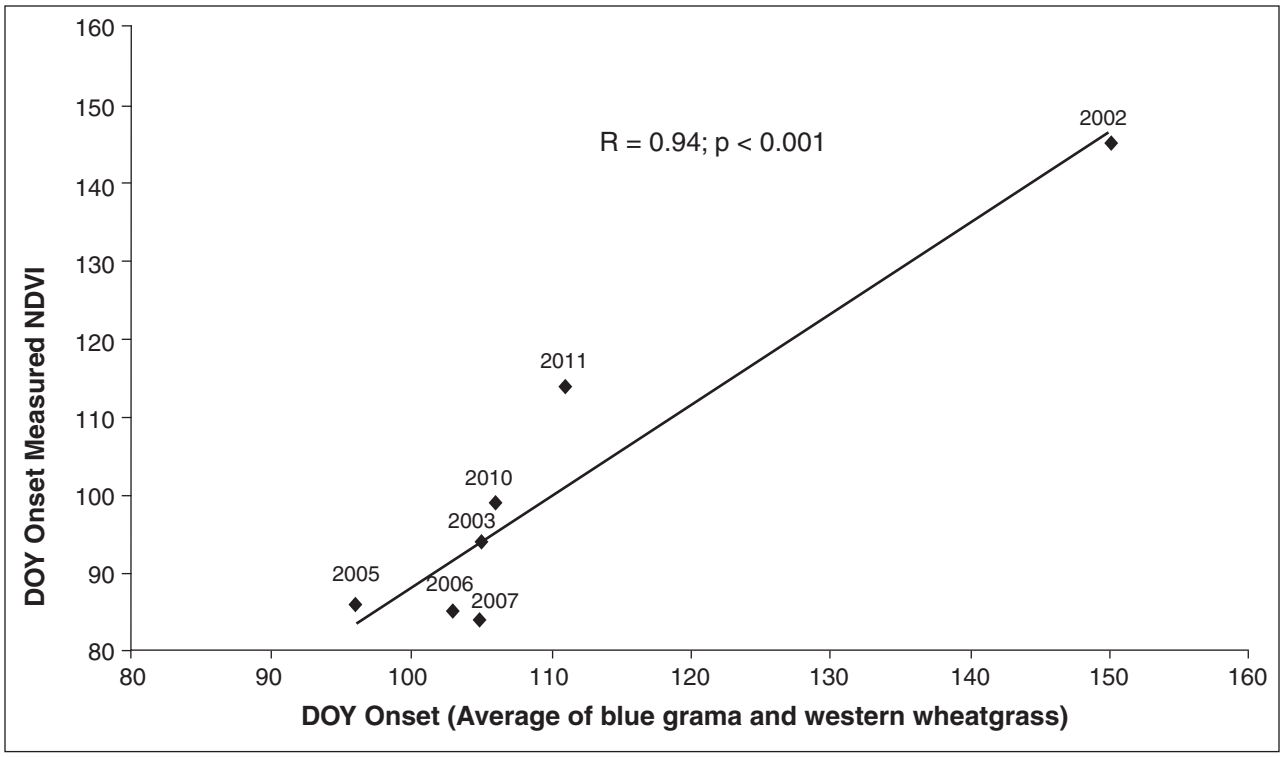

Figure S1. Day of year (DOY) of onset of spring for measured NDVI and field observations with Pearson correlation coefficient and *p*-value. Line is ordinary least squares regression line to aid in guiding the eye.

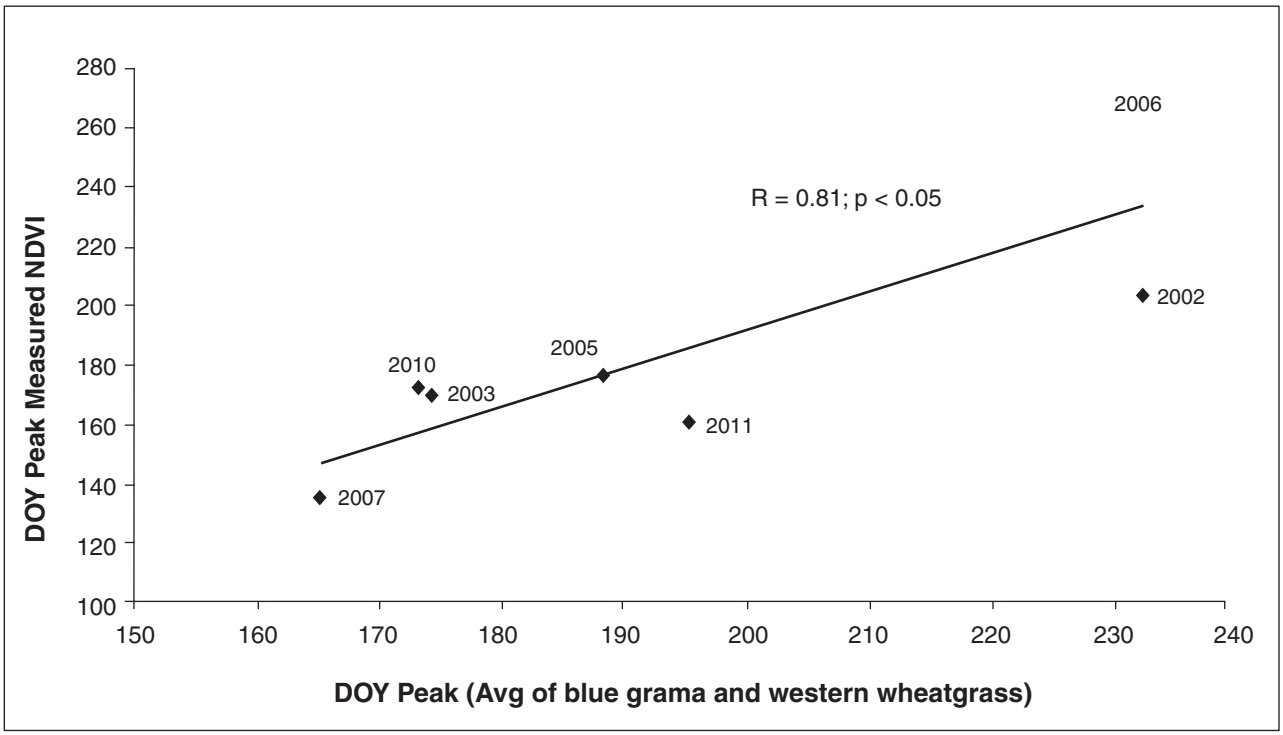

Figure S2. Day of year (DOY) of peak greenness for measured NDVI and field observations with Pearson correlation coefficient and *p*-value. Line is ordinary lease squares regression line to aid in guiding the eye.

TABLE S2. Mean fixed effects and standard errors (in parentheses) for ST (accumulated soil growing degree days), ST^2, SW (accumulated soil water days), SW^2, and ST · SD (interaction term) from the temperature only, water only, and full models.

	Temperature only	Water only	Full
	Equation 2	Equation 3	Equation 4
(Intercept)	0.616 (0.017)***	1.454 (0.510)**	0.530 (0.079)***
ST	0.026 (0.020)		−0.289 (0.248)
ST^2	−0.334 (0.067)***		0.140 (0.171)
SW		−5.188 (3.368)	1.045 (0.871)
SW^2		−13.014 (7.277)*	3.640 (2.631)
ST · SW			−2.350 (1.307)*

Note: Significance levels are indicated by asterisks: ***$p < 0.001$, **$p < 0.01$, and *$p < 0.1$.

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