



Semi-arid vegetation response to antecedent climate and water balance windows

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Keywords

Climate change; Grazing; Normalized difference vegetation index; Pulse response; Soil moisture; Water balance

Nomenclature

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Abstract

Questions: Can we improve understanding of vegetation response to water availability on monthly time scales in semi-arid environments using remote sensing methods? What climatic or water balance variables and antecedent windows of time associated with these variables best relate to the condition of vegetation? Can we develop credible near-term forecasts from climate data that can be used to prepare for future climate change effects on vegetation?

Location: Semi-arid grasslands in Capitol Reef National Park, Utah, USA.

Methods: We built vegetation response models by relating the normalized difference vegetation index (NDVI) from MODIS imagery in Mar–Nov 2000–2013 to antecedent climate and water balance variables preceding the monthly NDVI observations. We compared how climate and water balance variables explained vegetation greenness and then used a multi-model ensemble of climate and water balance models to forecast monthly NDVI for three holdout years.

Results: Water balance variables explained vegetation greenness to a greater degree than climate variables for most growing season months. Seasonally important variables included measures of antecedent water input and storage in spring, switching to indicators of drought, input or use in summer, followed by antecedent moisture availability in autumn. In spite of similar climates, there was evidence the grazed grassland showed a response to drying conditions 1 mo sooner than the ungrazed grassland. Lead times were generally short early in the growing season and antecedent window durations increased from 3 mo early in the growing season to 1 yr or more as the growing season progressed. Forecast accuracy for three holdout years using a multi-model ensemble of climate and water balance variables outperformed forecasts made with a naïve NDVI climatology.

Conclusions: We determined the influence of climate and water balance on vegetation at a fine temporal scale, which presents an opportunity to forecast vegetation response with short lead times. This understanding was obtained through high-frequency vegetation monitoring using remote sensing, which reduces the costs and time necessary for field measurements and can lead to more rapid detection of vegetation changes that could help managers take appropriate actions.

Introduction

Semi-arid ecosystems are especially susceptible to climate and land-use impacts and require careful management to avoid irreversible changes in vegetation composition and associated water, energy and nutrient cycles (Briske et al. 2006). In the southwestern US, semi-arid regions are projected to be hotter and drier (Seager et al. 2007), which

will affect vegetation composition and condition across broad geographic extents. These impacts to vegetation will add considerable stress to ecological systems, even in protected areas where land-use stressors are minimized (Cook et al. 2015). Changes in vegetation composition and condition affect biodiversity and economic services derived from forage production in these landscapes (Miller et al. 2011; Ault et al. 2014; Briske et al. 2015). When biotic

(e.g. herbivory) and abiotic (e.g. climate) conditions exceed plant physiological tolerances or response capacities, thresholds can be crossed that result in new, often undesirable ecological states. High frequency vegetation monitoring over broad areas can improve our ability to track abrupt and gradual vegetation responses to climate and land use, and provide managers with an early warning of approaching thresholds. Although not frequently implemented, this type of monitoring would ideally be used to generate forecasts of the near-term condition of vegetation at management-relevant time scales (Clark et al. 2008). Anticipating geographically specific vegetation changes can help managers mitigate stressors and plan restoration activities that provide more time for adaptation strategies to work (Briske et al. 2015).

Traditional plot-based range monitoring techniques can be effective for understanding how climate and livestock grazing influence vegetation (Munson et al. 2016). However, diverse landscapes and infrequent ground-based measurements often preclude tracking the dynamic fluctuations of vegetation that occur on seasonal or monthly time scales, which can result in a 'wait and see' management paradigm. Unfortunate outcomes from this approach can be lost opportunity to mitigate unwanted shifts in vegetation and irreversible environmental damage (Alhamad et al. 2007). Vegetation is water-limited in semi-arid environments, and understanding vegetation response to climate is complicated by time lags after weather events and the duration of antecedent conditions such as sustained drought or periods of wetness that affect the timing and magnitude of plant growth in the current and following years (Richard & Pocard 1998; Fabricante et al. 2009; Richard et al. 2012). In semi-arid environments, cycles in vegetation productivity have been linked to precipitation legacies from previous years and pulse-reserve responses that describe accrual of biological capital (leaves, roots, seeds) in wet years that set the stage for response in following years (Reynolds et al. 2004; Sala et al. 2012). Such lag and memory effects need explicit consideration in long-range planning and management of semi-arid lands (Milchunas et al. 1994).

Grazing is a common land use in semi-arid regions and interacts with climate to affect vegetation biomass and composition. Vegetation response to climate and grazing may vary by precipitation regime, functional type (e.g. grass vs shrub), soil type and the intensity and duration of grazing (Milchunas et al. 1994; Todd et al. 1998; Robinson et al. 2012). From a management perspective, complex interactions among these factors demonstrate the need for broad-scale monitoring techniques that account for variation in these factors, which are difficult to encompass with plot-based studies.

Remote sensing offers high-frequency and broad-scale observations that can improve understanding of vegetation response to environmental conditions with high spatiotemporal variation (Fuller & Prince 1996; Moreno-de las Heras et al. 2015). Yet numerous challenges exist for remote sensing of vegetation condition in semi-arid landscapes. These obstacles include noisy observations, relatively weak signals, low vegetation cover with bright soil backgrounds, high inter-annual variability in vegetation greenness, lagged vegetation response to climate, and little to no vegetation green-up in drought years (de Beurs & Henebry 2010). Despite these challenges, remote sensing has potential to help fill important spatial and temporal gaps in semi-arid vegetation monitoring programmes. When coupled with ground-based observations that describe plant species assemblage and land use in the remote sensing footprint, more nuanced interpretations of vegetation relationships with climate are possible than when using remote sensing methods alone (Moreno-de las Heras et al. 2015). These interpretations have value for informing management decisions that may benefit by flexibly responding to current and near-term forage conditions (Alhamad et al. 2007).

Satellite-derived proxies for vegetation condition, such as the normalized difference vegetation index (NDVI), have been used to study climate and grazing effects on vegetation in semi-arid environments for several decades (Fuller & Prince 1996; Paruelo & Lauenroth 1998; Todd et al. 1998; Moreno-de las Heras et al. 2015). However, few studies investigated the multivariate suite of water balance factors and their antecedent conditions in semi-arid environments that, on a monthly basis, may be more closely related to vegetation response than climate factors (Fuller & Prince 1996; Alhamad et al. 2007; Huber et al. 2011; Campo-Bescós et al. 2013). Water balance metrics may be more directly related to plant physiological response at monthly time scales than precipitation alone because water balance estimates temporal aspects of both stored soil moisture (SM) and water deficit that regulate plant growth (Rosenzweig 1968; Stephenson 1998) in semi-arid environments. Accounting for SM storage becomes increasingly important in water-limited environments because it helps maintain plant productivity through dry seasons and years (Bisigato et al. 2013; Campo-Bescós et al. 2013).

The primary objectives of this research were to: (1) determine the timing of antecedent climate or water balance predictors of monthly NDVI in proximal ungrazed and grazed semi-arid grasslands; (2) identify differences in response to antecedent conditions that may be related to grazing history and vegetation composition; and (3) evaluate accuracy of near-term forecasts of monthly NDVI for management planning.

Methods

Study area

Capitol Reef National Park is situated in the Colorado Plateau physiographic province in south-central Utah, USA (Fig. 1). This semi-arid park has a mean annual precipitation (P) of approximately 240 mm, which is composed of cool season (October–March) frontal precipitation (52% of annual P) and warm season (July–September) convective P (30% of annual P) (Table 1; Hereford et al. 2002). We focus on two perennial grassland management units that each consist of the same three ecological sites; Semi-desert Alkali Sandy Loam, Semi-desert Sand and Semi-desert Sandy Loam (U. S. Department of Agriculture, Natural Resources Conservation Service. 2004; Draft of Soil Survey of Capitol Reef National Park: Parts of Kane and Garfield

Counties, Salt Lake City, UT). Grouping ecological sites by management unit also increased the pixel sample size, creating a more favourable signal-to-noise ratio for observations in semi-arid environments (de Beurs & Henebry 2010). Both grasslands were grazed with livestock, beginning in the early 1900s, but one has not been grazed since 2000 (ungrazed Cathedral grassland: 7.3 km²; Fig. 1), while the other is actively grazed October through May (grazed Hartnet grassland: 7.2 km²). These two grasslands are part of a long-term monitoring programme that began in 2008, aimed at understanding historical grazing and climate effects on semi-arid vegetation, and they share similar physical conditions because of their close proximity (Witwicki 2013). Both grasslands have deep (>150 cm) soils on relatively level depositional surfaces that accumulated sandy and gravelly sediments from surrounding

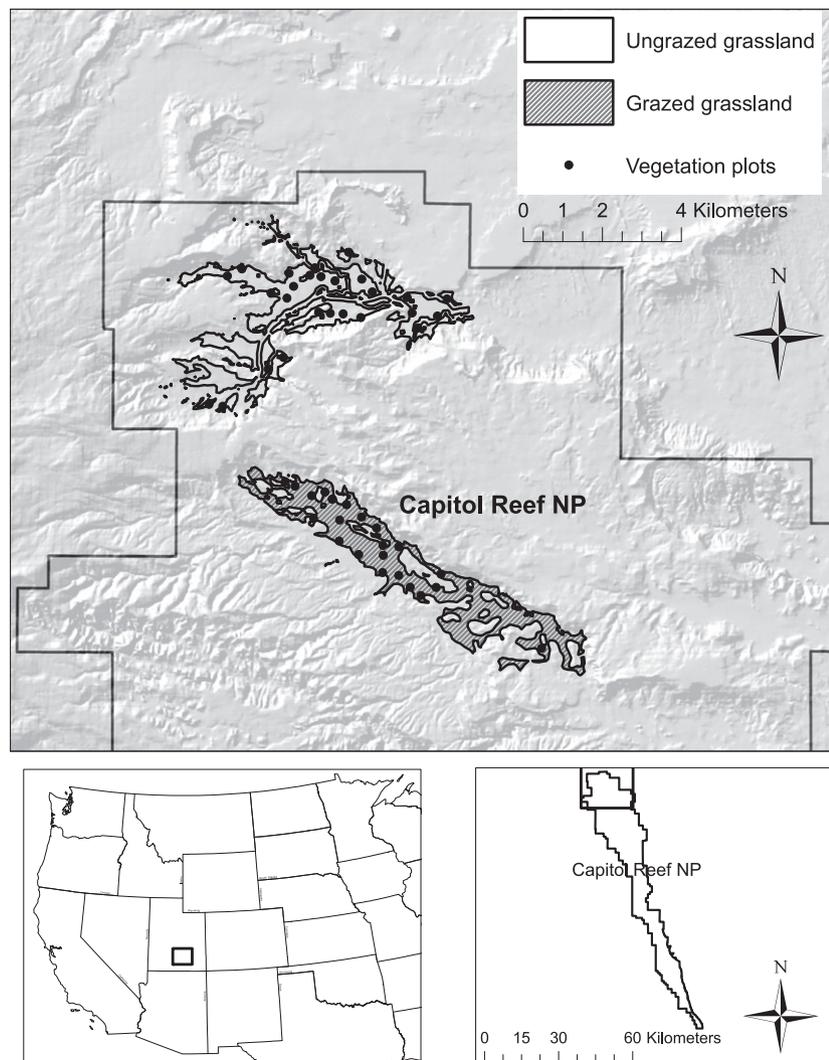


Fig. 1. The grazed and ungrazed grasslands in the northern region of Capitol Reef National Park, US. Dots represent locations of permanent vegetation plots used to characterize species composition and cover.

Table 1. Seasonal and annual average climate and water balance for the grasslands (2000–2013).

Grassland	Period	NDVI	P (mm)	T (°C)	AET (mm)	GDD (°C)	D (mm)	SM (mm)
Ungrazed	Spring	0.146 (0.06)	58 (0.08)	9 (0.49)	97 (0.04)	491 (0.24)	52 (0.35)	35 (0.28)
	Summer	0.166 (0.01)	58 (0.17)	21 (0.09)	80 (0.07)	1562 (0.04)	250 (0.04)	5 (0.85)
	Autumn	0.169 (0.04)	79 (0.11)	10 (0.68)	62 (0.11)	575 (0.29)	75 (0.26)	10 (0.56)
	Annual	0.157 (0.05)	251 (0.28)	10 (0.06)	247 (0.25)	2631 (0.06)	383 (0.19)	15 (0.64)
Grazed	Spring	0.134 (0.06)	51 (0.08)	9 (0.49)	86 (0.04)	510 (0.24)	66 (0.35)	28 (0.28)
	Summer	0.147 (0.01)	56 (0.17)	22 (0.09)	74 (0.07)	1585 (0.04)	261 (0.04)	4 (0.85)
	Autumn	0.137 (0.04)	75 (0.11)	10 (0.68)	58 (0.11)	589 (0.29)	80 (0.26)	10 (0.56)
	Annual	0.136 (0.07)	230 (0.3)	10 (0.06)	226 (0.27)	2687 (0.06)	416 (0.18)	13 (0.71)

Values in parentheses are coefficients of variation. Spring months are March–May; summer months are June–August; autumn months are September–November. Annual values include winter months December–February. NDVI is the normalized difference vegetation index; *P* is precipitation; *T* is temperature, AET is modelled actual evapotranspiration; GDD is accumulated growing degree-days; *D* is water deficit; SM is soil moisture.

uplands. The grasslands were similar with respect to water-holding capacity in the top 1 m of soil (grazed = 99 mm; ungrazed = 90 mm), which we calculated as a spatially weighted average from the ecological site components (Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture; Web Soil Survey available at <http://websoilsurvey.nrcs.usda.gov/> Accessed 24 May 2013).

Vegetation and environmental measurements

Vegetation

Randomly located permanent vegetation plots (22 grazed and 26 ungrazed) were sampled once annually in May or Jun from 2008 to 2013 (Fig. 1). Vegetation plots consisted of three parallel, 50-m transects spaced 25 m apart. A point-intercept method was used to record cover of plant

species at any height in the canopy at 0.5-m intervals along each transect. We report species abundance as cover, which is the count of points where each species was detected at a plot divided by the sum of all points sampled at a plot (Table 2). Since 2000 there have been no fires or notable vegetation transitions according to park staff, but there may have been gradual increases in C₃ grass cover in the ungrazed grassland after grazing ceased. Here we account for grazing as the major disturbance by contrasting grazed and ungrazed grassland response.

Satellite imagery

A time-series of 16-d maximum value composite, 250-m resolution MODIS images (MOD13Q1; LPDAC 2011) from 2000 through 2013 were processed to remove low quality pixel values that were caused by clouds, aerosols or snow

Table 2. Percentage cover of the seven most abundant live plant species at field plots monitored during growing seasons 2008–2013.

	Scientific Name	Common Name	Functional Group	Photosynthetic Path	Grazer Palatability ¹	% Cover
Ungrazed Grassland	<i>Sporobolus airoides</i>	Alkali sacaton	Perennial grass	C ₄	Medium	3.9
	<i>Achnatherum hymenoides</i>	Indian ricegrass	Perennial grass	C ₃	High	2.6
	<i>Bouteloua gracilis</i>	Blue grama	Perennial grass	C ₄	High	1.6
	<i>Gutierrezia sarothrae</i>	Broom snakeweed	Shrub		Low	1.0
	<i>Muhlenbergia pungens</i>	Sandhill muhly	Perennial grass	C ₄	Low	0.8
	<i>Opuntia</i> sp.	Prickly pear (sp).	Sub-shrub		Low	0.8
	<i>Pleuraphis jamesii</i>	Galleta grass	Perennial grass	C ₄	High	0.8
	Other					4.7
	Total				16.1	
Grazed Grassland	<i>Sporobolus airoides</i>	Alkali sacaton	Perennial grass	C ₄	Medium	1.9
	<i>Pleuraphis jamesii</i>	Galleta grass	Perennial grass	C ₄	High	1.4
	<i>Achnatherum hymenoides</i>	Indian ricegrass	Perennial grass	C ₃	High	1.4
	<i>Krascheninnikovia lanata</i>	Winterfat	Shrub		High	0.9
	<i>Gutierrezia sarothrae</i>	Broom snakeweed	Shrub		Low	0.8
	<i>Atriplex confertifolia</i>	Shadscale	Shrub		High	0.7
	<i>Bouteloua gracilis</i>	Blue grama	Perennial grass	C ₄	High	0.4
	Other					2.8
	Total				10.3	

¹USDA NRCs PLANTS database. http://plants.usda.gov/about_plants.html [Accessed 7 Jul 2014].

cover. The NDVI was calculated from visible and near infrared reflectance as,

$$\text{NDVI} = \frac{(\rho_{\text{NIR}} - \rho_R)}{(\rho_{\text{NIR}} + \rho_R)}, \quad (1)$$

where ρ_{NIR} is reflectance in near infrared band (0.841–0.876 μm) and ρ_R is reflectance in the red band (0.620–0.670 μm) (Solano et al. 2010). Pixels within each grassland ($n = 157$ ungrazed; $n = 138$ grazed) were spatially averaged at each time step to create a 16-d time series of NDVI from 2000 through 2013 for each grassland. Missing values in the 16-d time series only occurred in December through February due to clouds or snow and were linearly interpolated before smoothing (Verbesselt et al. 2009). We used Timesat software to implement a three period Savitzky-Golay moving window filter to smooth high-frequency noise that remained in the time series (Jonsson & Eklundh 2004; Moreno-de las Heras et al. 2015). The interpolation to monthly time step at the end of each month was performed using a three period moving window linear regression on 16-d NDVI values. The smoothing and interpolation procedures preserved the timing and magnitude of NDVI variation while minimizing noise that was not likely related to vegetation phenology (Jonsson & Eklundh 2004; Verbesselt et al. 2009; Fig. 2).

In order to evaluate annual relationships between NDVI as a surrogate for annual net primary productivity (ANPP), we calculated the integrated annual NDVI (iNDVI). Since NDVI includes a component of reflectance from bare soil in minimally vegetated areas, we minimized the soil contribution to NDVI by subtracting the minimum growing season NDVI for each grassland (ungrazed = 0.11; grazed = 0.10) from each monthly NDVI value before calculating iNDVI (as per Moreno-de las Heras et al. 2015):

$$i\text{NDVI}_y = \sum_{m=\text{Apr}}^{m=\text{Oct}} (\text{NDVI}_m - \text{NDVI}_{\text{min}}), \quad (2)$$

where, NDVI_m is monthly NDVI from April through October and NDVI_{min} is the minimum NDVI value for the 2000–2013 period.

Climate and water balance

Daily precipitation (P) and temperature (mean [T_{mean}], minimum [T_{min}] and maximum [T_{max}]) data for the grasslands were obtained from Daymet interpolated 1-km climate grids (Thornton et al. 1997; Daymet: Daily surface weather on a 1-km grid for North America, 1980–2013, <http://daymet.ornl.gov/>, accessed 29 Apr 2014). We constructed time series of these climate variables from single

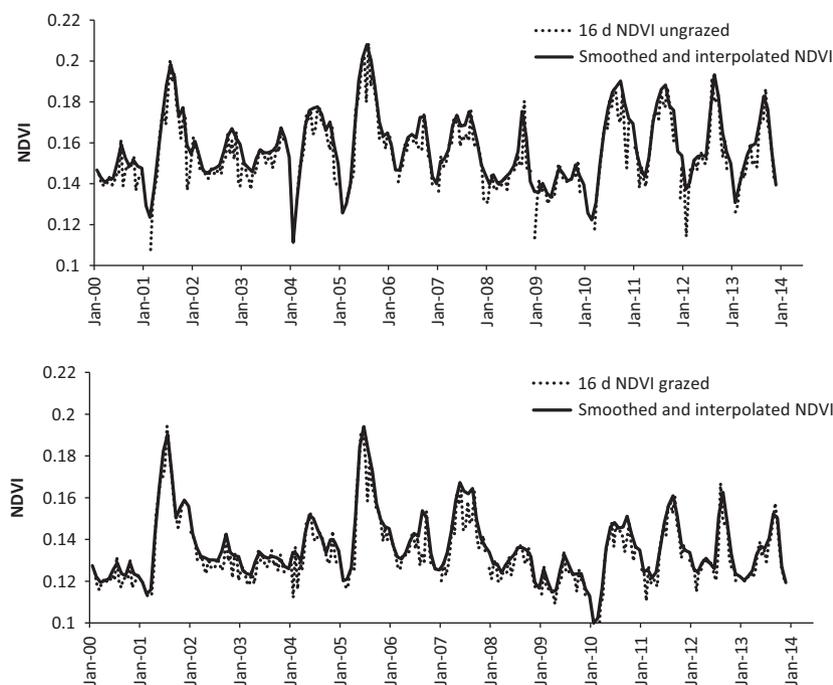


Fig. 2. Seasonal and inter-annual variation in NDVI in (a) ungrazed grassland and (b) grazed grassland in Capitol Reef National Park, US. Lines represent the effects of gap-filling and interpolating 16-d NDVI to monthly time step that matched temporal resolution of monthly water balance. Gaps in 16-d time series were due to screening of low quality pixel values. The NDVI response in the two grasslands is strongly correlated ($r^2 = 0.48$).

pixels within our study areas because our water balance model was point-based and in practice managers often rely on climate data from individual stations to make inferences about vegetation condition.

Growing degree-days (GDD) is the daily sum of heat accumulation for the month ($^{\circ}\text{C}$), which is related to phenological development (Wang et al. 2003). We calculated GDD as described by McMaster & Wilhelm (1997),

$$\text{GDD} = \left[\left(\frac{T_{\max} + T_{\min}}{2} \right) \right] - T_{\text{base}}, \quad (3)$$

where $T_{\text{base}} = 4.44$ $^{\circ}\text{C}$, the temperature below which grass physiological activity ceases (Wang 1960).

We used mean monthly temperature and monthly precipitation as inputs to a Thornthwaite-type monthly water balance model to estimate water input to the soil, SM storage and loss of water via evapotranspiration (Dingman 2002). The monthly water balance equations were identical to Lutz et al. (2010) with one exception. In our model we calculated the water balance for each year separately and carried December SM over to the following Jan to account for soil as a capacitor of moisture as suggested by Bisigato et al. (2013).

Soil moisture is the quantity of water stored in the soil at the end of each month (mm). Potential evapotranspiration (PET) is the amount of water that could be evapotranspired with available energy if water availability was unlimited to a short grass. Actual evapotranspiration (AET) is the monthly upward loss of water from soil via transpiration and evaporation, which is limited by SM availability. Deficit (D), a positive value measure of drought stress, is the amount of additional water vegetation would use if it were available, calculated as the difference between monthly PET and AET (Stephenson 1998).

Data reduction

The NDVI, water balance and climate data were aggregated or interpolated to create monthly data sets of all variables. Relying on previous studies, we chose a set of candidate predictors of NDVI that affect vegetation growth in semi-arid regions (Huber et al. 2011; Campo-Bescós et al. 2013): (1) precipitation (P); (2) precipitation and temperature additive interaction (P_T); (3) growing degree days (GDD); (4) SM; (5) AET; and (6) water deficit (D). We then calculated antecedent conditions prior to each NDVI observation according to Wang et al. (2003) by summarizing climate and water balance values backward in a step-wise monthly fashion up to 2 yrs prior to each NDVI observation,

$$C_{(m)} = \sum_{j=0}^m C_j, \quad \text{for variables } P, \text{ AET, } D \text{ and GDD}, \quad (4)$$

and

$$C_{(m)} = \frac{\sum_{j=0}^m C_j}{m} \quad \text{for variables SM and } T, \quad (5)$$

where C_j is the climate or water balance term used to model NDVI for month j , m is months prior to NDVI observation. In the case when $m = 0$ the climate or water balance term is the value for the month concurrent with the NDVI observation. In the case where $m = 24$, the climate or water balance term is the sum (eqn 4) or average (eqn 5) of monthly values backward in time for 2 yrs prior to the NDVI observation. The magnitude of m represents the duration of accumulation for climate or water balance terms used in models of NDVI response. The SM predictor was computed as an average because it has an upper limit based on physical properties that affect soil water-holding capacity. Temperature was considered cumulatively as GDD and as an average for its interaction with precipitation.

Analysis

Since vegetation response lags behind weather, or alternatively weather leads vegetation response, we included predictor lead times up to 5 mo (including zero lead) in our analysis (Wang et al. 2003). Duration zero and lead zero represent climate or water balance conditions in the month concurrent with NDVI observation, whereas duration one represents the sum of current and previous month and lead one indicates conditions 1 mo prior to the NDVI observation. We used simple linear regression in R (R Foundation for Statistical Computing, Vienna, AT)

$$\text{NDVI}_j = \hat{\beta}_{0,j} + \hat{\beta}_{1,j} C_{(m),l} + \varepsilon_i \quad (6)$$

where $C_{(m),l}$ is the climate or water balance variable accumulated across m months prior to the NDVI observation via eqns 4 and 5 where $m = 0, \dots, 24$, leading NDVI by l months where $l = 0, \dots, 4$, and $\hat{\beta}_{0,j}$ is an estimated parameter for month j , we use j to denote separate monthly NDVI models where $j = 1, \dots, 12$, ε_i is the residual error term for a yearly observation in month j (where $i = 2000, \dots, 2010$) assumed to be independent and normally distributed. For example, we built a cross-year June NDVI response model by regressing June NDVI values (one from each year; $n = 11$) on climate data representing different durations and leads preceding each annual June NDVI value.

We tested for autocorrelation in yearly residuals using the Durbin Watson test statistic (R package *car*; Fox & Weisberg 2011) and visual inspection of autocorrelation functions for each predictor by month. We found no strong evidence of autocorrelation within model residuals. The number of monthly models for each month, called the model set (five leads, 25 durations and six predictors = 750) is greater than the monthly model cross-year response ($n = 11$). As such, we evaluated monthly model sets using an information theoretic approach to identify a plausible set of predictors, durations and lead times that may be useful indicators of NDVI response for each month. We used Akaike's information criterion adjusted for small sample size (AIC_c) as a measure of model fit, and the ΔAIC_c as a means of model comparison within each monthly model set. The AIC_c for each model was calculated as,

$$AIC_c = n \log(\hat{\sigma}^2) + 2K + \frac{2K(K+1)}{n-K-1}, \quad (7)$$

where n was sample size, $\hat{\sigma}^2$ is model variance and K is total number of estimated regression parameters, including the intercept and $\hat{\sigma}^2$.

The ΔAIC_c for each model was,

$$\Delta AIC_c = AIC_i - AIC_{\min}, \quad (8)$$

where AIC_i is AIC_c for model i and AIC_{\min} is the minimum AIC_c value for all models in the monthly model pool. We consider monthly models with $\Delta AIC_c < 4$ as having support by the data and are thus competitive candidate models (Burnham & Anderson 2002).

The information theoretic approach helps identify a pool of plausible monthly models, but does not eliminate the possibility of selecting spurious models by chance, and it can be difficult to interpret when there are many competitive models. We used k -fold validation as a tool to assess the reliability of our near-term forecasts and our inferences regarding climatic and water balance variables as related to monthly NDVI (Maindonald & Braun 2007). We performed 100 iterations of the analysis, which involved randomly selecting three holdout years of NDVI climate and water balance, building and selecting competitive models with 11 yrs of data, and then making forecasts of monthly NDVI for the holdout years (described in the next section). Using these iterations, we identified the frequency of predictor variable occurrence as well as the most frequently occurring leads and durations by month. We computed the average NDVI forecast accuracy across all 100 iterations and then selected one of the iterations that had forecast accuracy similar to the 100 iteration average to conservatively

demonstrate forecast accuracy. The iterations demonstrate robustness to selection of holdout years and competitive models and a more accurate estimate of forecast performance. Using the representative forecast group of 3 yrs, we use heat maps to demonstrate competitive predictors and their associated antecedent windows that were most influential in determining monthly NDVI response by grassland.

Forecasts

In our k -fold validation we evaluated two forecasting methods (Yu et al. 2015). The first was a multi-model average of the most competitive climate/water balance predictors. Multi-model average forecasts for each month were calculated as,

$$\hat{\theta} = \sum_{i=1}^R w_i \hat{\theta}_i, \quad (9)$$

where $\hat{\theta}$ is the multi-model estimate of NDVI for a given month in a holdout year, R is the number of competitive monthly models and w_i are Akaike weights which sum to 1 and are calculated as,

$$w_i = \frac{\exp(-(1/2)\Delta AIC_{c_i})}{\sum_{r=1}^R \exp(-(1/2)\Delta AIC_{c_r})}, \quad (10)$$

where ΔAIC_{c_i} is the ΔAIC_c for each of the competitive monthly models.

The second forecast method was a naïve forecast calculated using a 'NDVI climatology' that was the monthly average NDVI from years in each iteration of the model building set. If our climate/water balance multi-model average forecast performs better than an average monthly NDVI forecast, we confirm that antecedent climate and water balance help explain NDVI. We evaluated the performance of both forecast methods using root mean square error (RMSE) as an indicator of fit between observed and modelled NDVI (Wang et al. 2007).

Results

Vegetation composition

The plant species with the highest cover in the grazed grassland were *Sporobolus airoides* (alkali sacaton) a C_4 grass; *Pleuraphis jamesii* (galleta grass), a C_4 grass; *Achnatherum hymenoides* (Indian ricegrass), a C_3 grass. In the ungrazed grassland, *S. airoides* (alkali sacaton), *A. hymenoides* (Indian rice grass) and *Bouteloua gracilis* (blue grama), a C_4 grass, had the highest cover (Table 2). Species

richness was 7.5 and 10.5 species-plot⁻¹ in the grazed and ungrazed grassland, respectively.

The NDVI satellite Imagery

There was high inter- and intra-annual variability in NDVI (Fig. 2) that exhibited a strong correlation between the grasslands ($r^2 = 0.48$). However, the generalized seasonal pattern in both grasslands was green-up in March through May, peak greenness between June and September, followed by gradual decline as vegetation senesced in September through November (Fig. 2, Appendix S1). In some years monthly NDVI had a second peak between Aug and October (2001, 2007 and 2010). During the study period, NDVI annual average in the grazed grassland was 0.136 ($cv = 0.072$), which was less than ($P < 0.0001$) the ungrazed grassland NDVI annual average of 0.157 ($cv = 0.051$; Table 1).

Climate and water balance

Seasonal patterns in median climate and water balance were apparent in spite of high inter-annual variability (Table 1, Appendix S1). Recharge of SM occurred October through March during vegetation senescence and dormancy (Appendix S1; December, January, February not shown). Stored moisture was utilized to near depletion by September, however convective monsoon storms in July through October provided moisture pulses in most years (Table 1, Appendix S1; Notaro et al. 2010; Forzieri et al. 2011). May and June were the driest months with an average P of 8 to 14 mm month⁻¹. Variation in annual AET was similar to annual variation in P , as 98% of P was returned to the atmosphere via AET (Table 1).

Precipitation legacy effects on NDVI

Multi-year P legacies were apparent in both grasslands. In the ungrazed grassland, years 2005 and 2011 had the highest annual i NDVI and were preceded by years with the highest annual P (Fig. 3). On the other hand, three consecutive years of below-average P from 2007 through 2009 resulted in the lowest i NDVI in 2009 (71% of average), which was followed by the year of highest annual P in 2010 that only brought productivity back up to average (101%). It took another year of above average P in 2011 to raise productivity to the maximum observed in the study at 119% of average in 2011. Similar patterns were observed in the grazed grassland, but after the below-average 2007–2009 P years, the 2011 i NDVI response (104%) was not as strong.

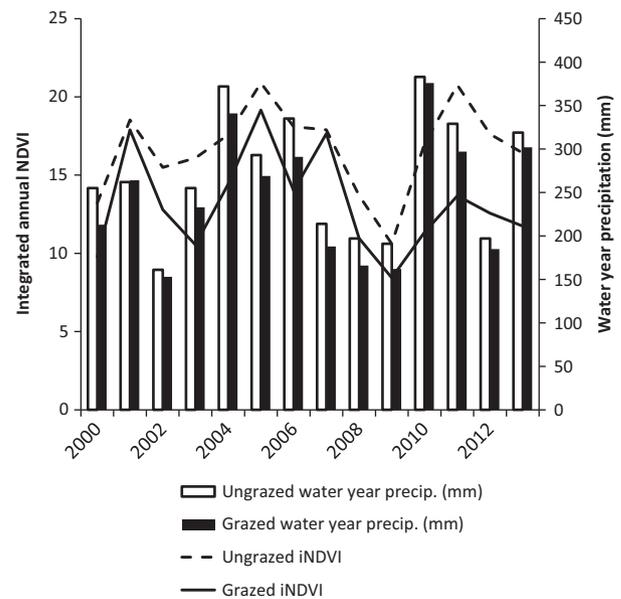


Fig. 3. Inter-annual variation in precipitation and productivity estimated as the integrated annual NDVI (i NDVI from eqn 2) in the grazed and ungrazed grasslands, Capitol Reef N.P., US Water year is designated as the year it ends and is the sum of P from October through September in the following year.

Patterns in competitive monthly model iterations

Based on holdout iterations, competitive monthly models included SM most frequently (61.3%), followed by D (14.6%), P_T (10.2%), P (7.7%), AET (3.7%) and GDD (2.5%). Seasonally, vegetation response models for both grasslands indicate antecedent water input and storage were the best predictors in the early growing season (P , P_T , SM), switching to indicators of drought, input or use in the mid-season (D , P , AET), followed by antecedent moisture availability (SM) late in the growing season (Fig. 4a, Appendix S2).

The most frequent lead times in vegetation response models were zero to 2 mo from March through July (Fig. 4b). However, in May and June, leads of 3 to 4 mo were important in the grazed grassland. Beginning in August, both short leads and longer leads were common in models for the remainder of the growing season.

The window durations when predictors become important in the ungrazed grassland generally increased from <3 mo to 1 yr as the growing season progressed from March through October. In the grazed grassland durations increased from 3 to 18 mo as the season progressed from May through October (Fig. 4c). Durations >12 mo spanning multiple growing seasons occurred in most monthly response models for both grasslands. Dual peaks separated

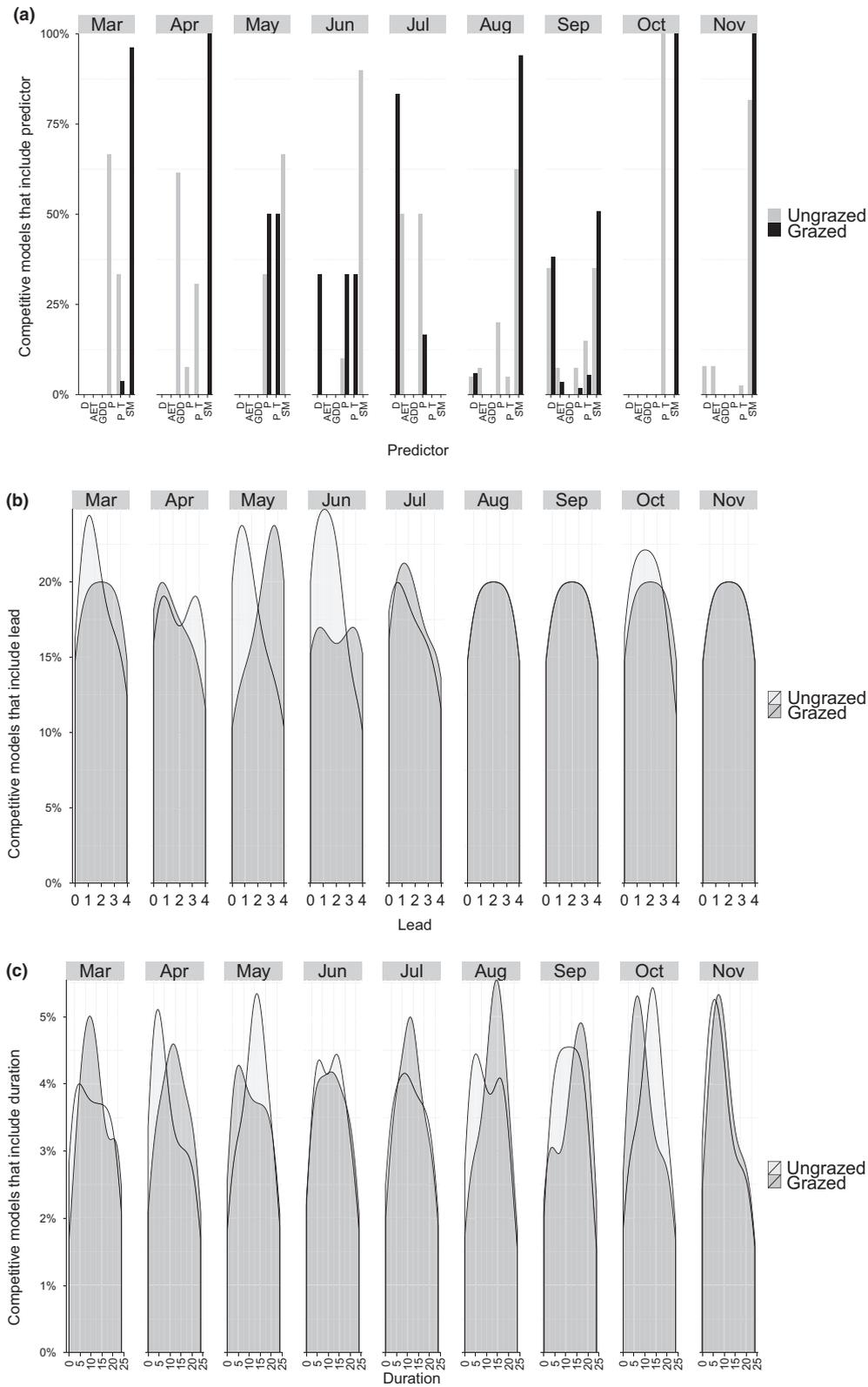


Fig. 4. Predictors and antecedent window timing in competitive models for 100 iterations of the model-building process. (a) Frequency of predictor occurrence in competitive monthly models ($\Delta AIC_c < 4$); (b) frequency of lead in competitive monthly models, with density shown as shaded area; and (c) frequency of duration in competitive monthly models, with density shown as shaded area.

by 12 mo suggest annual cycles in climate, water balance and phenology are coupled (Fig. 4c August and June panels, ungrazed).

Forecasts

The 3-yr multi-model climate/water balance forecasts for 100 iterations (grazed $rmse = 0.009$; ungrazed $rmse = 0.008$) performed better on average than naïve forecasts across the analysis iterations (grazed $rmse = 0.013$; ungrazed $rmse = 0.012$; Appendix S2). We demonstrate time series forecasts of monthly NDVI with three holdout years (2001, 2005, 2010) that have forecast accuracy similar to the average over 100 iterations of the analysis process (Fig. 5).

Multi-model comparison

Using the representative holdout years 2001, 2005 and 2010, the predictors and antecedent conditions that were deemed competitive and statistically similar ($\Delta AIC_c < 4$) by month and grassland are presented in heat maps for the months representing early (May), middle (July) and end (October) of the growing season (Fig. 6). In May, a 13-month average of SM preceding the May NDVI observation was the best model ($r^2 = 0.70$) for the ungrazed grassland (Fig. 6a, Appendix S1). In contrast, the best

model ($r^2 = 0.90$) for the grazed grassland in May was P with lead 3 and duration 4, which represents P summed across November through February preceding the NDVI observation (Fig. 6b, Appendix S1). Similar interpretations can be made for summer months when AET and D are important and in autumn months when P_T and SM are important (Fig. 6c–f).

We note an important relationship between lead and duration in the heat maps, where many of the competitive monthly model leads and durations sum to a constant value that point to a narrowly defined window of time when climate or water balance were most important (Fig. 6). For example, in October the grazed allotment best model was SM with lead 0 and duration 8. Other competitive models included duration 7, lead 1; duration 6, lead 2; and duration 5 lead 3 (Fig. 6f). All of these lead and duration sums point to a window beginning in February where increase in SM forward in time since February is correlated with NDVI in October.

Discussion

Remote sensing

Many remote sensing studies have shown strong NDVI response to precipitation in semi-arid environments on an annual or seasonal basis (Paruelo & Lauenroth 1998; Wang et al. 2003; Nagler et al. 2007; Fabricante et al. 2009;

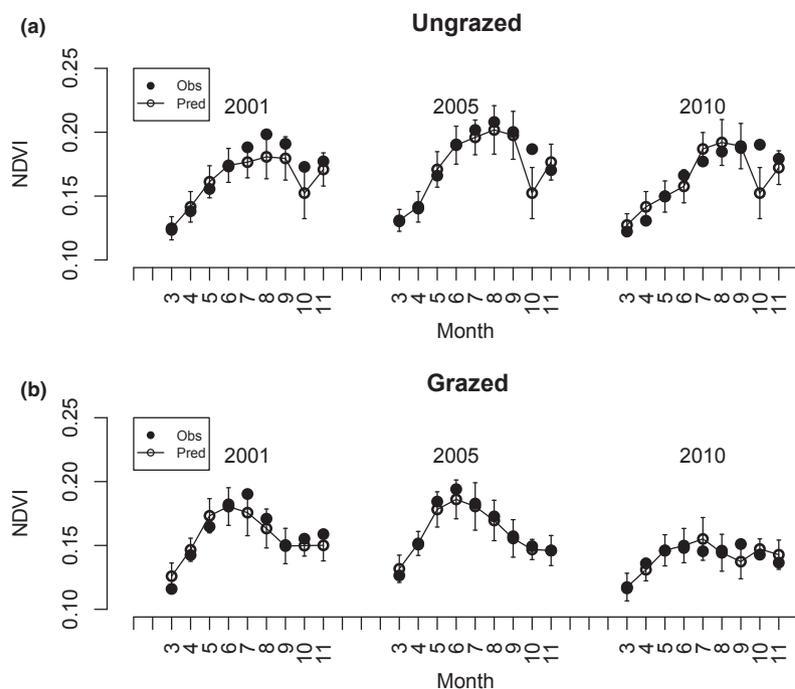


Fig. 5. Observed and multi-model forecast NDVI for holdout years 2001, 2005 and 2010 with 90% prediction intervals on monthly forecasts for (a) ungrazed grassland, 3-yr $rmse = 0.010$ and (b) grazed grassland, $rmse = 0.008$.

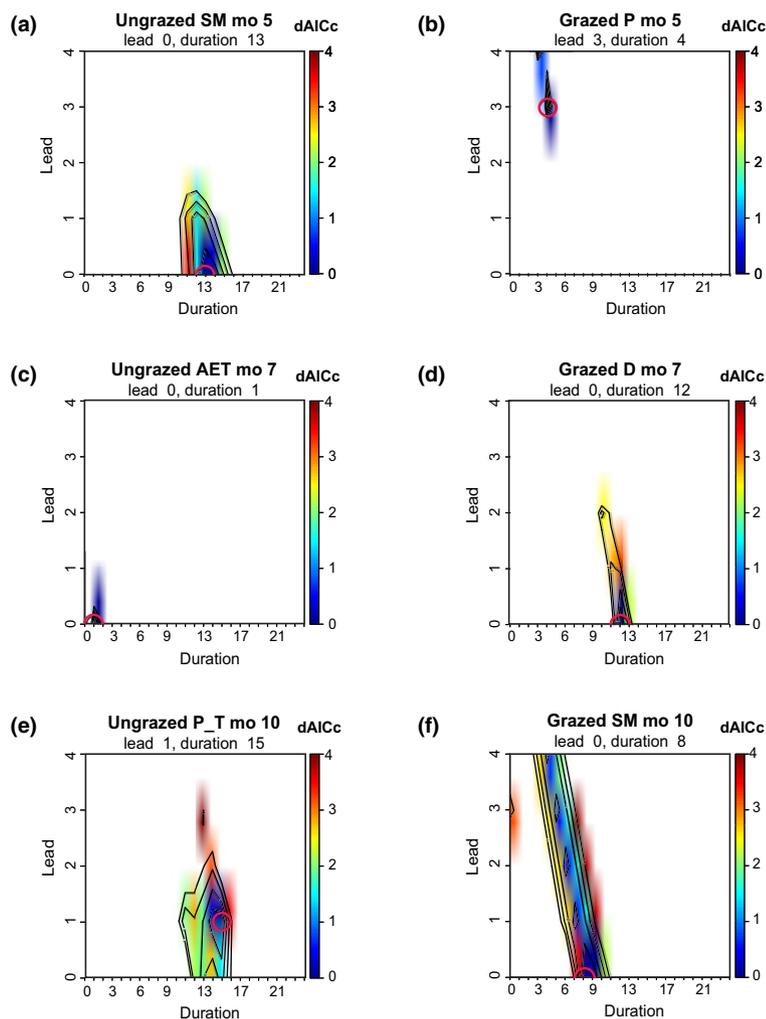


Fig. 6. Spring (top row), summer (middle row) and autumn (bottom row) heat maps of ΔAIC_c values <4 for predictors of NDVI and their antecedent conditions for the two grasslands with holdout years 2001, 2005 and 2010. Text and red circle indicate top model with smallest AIC_c . Areas in maps with no colour have $\Delta AIC_c > 4$. Left panels ungrazed, right panels grazed.

Jenerette et al. 2010; Huber et al. 2011; Moreno-de las Heras et al. 2015). Fewer studies have investigated relationships at monthly or more frequent intervals (Szilagyi et al. 1998; Philippon et al. 2005), and a very small number of studies have investigated multiple climate and water balance factors, including switches between the most important factors that can occur spatially or temporally (Notaro et al. 2010; Campo-Bescós et al. 2013). Although under studied previously, determining the influence of water availability on the condition of vegetation at high spatial and temporal resolution is required for understanding ecosystem processes and for effective management practices. Our results demonstrate that high annual, seasonal and monthly variations in NDVI in semi-arid environments can be largely explained with climate and water

balance predictors and their associated antecedent windows of time.

General patterns of NDVI response

Soil moisture, P , P_T and GDD (for ungrazed only) occurred most frequently in competitive models of NDVI response early in the growing season, consistent with findings of Muldavin et al. (2008), who found grasslands with C_3 species responded most strongly to winter accumulation of precipitation as SM and break from cold dormancy as temperatures warm in spring. As SM reserves became depleted into the summer months, competitive response models included AET and D , which represent immediate use or response to drought depending on the quantity of

monsoon precipitation. Late in the growing season, SM again occurred in competitive response models, which indicates that SM largely determines vegetation greenness at the end of the growing season. Interestingly, in months when SM and D were the best predictors, durations were generally long, which suggests that the storage of moisture and accumulation of water deficits most affected plant growth. This is consistent with the strong response of herbaceous vegetation in the Chihuahuan Desert to monsoon plus winter precipitation noted by Moreno-de las Heras et al. (2015) and Notaro et al. (2010). In contrast, in months where P , AET and GDD were competitive predictors, durations were generally short, which suggests that pulses of water input and use during the late summer monsoon season, and whether the temperatures are warm enough to grow in spring, have immediate effects on plant growth. Near-term response to monsoon precipitation in semi-arid areas was also noted in all the above studies. Inter-annual legacy effects noted in the inter-annual i NDVI time series were apparent in the monthly competitive models where durations centered on 12 mo were common for both grasslands.

For both grasslands, we found 0 to 3 mo leads in vegetation response models March through July that shifted to longer leads of 2 to 4 mo in August to November. The longer leads indicate vegetation response in those months was tied to conditions occurring earlier in the growing season, which suggested potential for forecasting end-of-season conditions several months in advance.

Seasonal switches

Water storage

In the grazed grassland, there was an early growing season response to SM that started in March and ended in May, which shifted to May and June in the ungrazed grassland. The earlier switch in the grazed grassland from SM to measures of water use (AET) or drought (D) in May and June, the two driest months, indicates the grazed grassland dried earlier in the year, or its vegetation assemblage was more sensitive to drier near-surface conditions and the ungrazed grassland was sustained longer by SM. July was the only month when SM was not found in competitive models for both grasslands. However, by August SM was important again, probably due to response of more deeply rooted vegetation with access to deeper SM (Munson et al. 2011).

Although the grazed grassland soils have higher water-holding capacity, the timing of switch in predictor variable from water use or drought was likely because annual P is 21 mm less in the grazed grassland, about 9 mm of which results from less winter P in the October through March SM recharge period (Table 1). This finding highlights vegetation sensitivity in these grasslands to small spatial differ-

ences in P during the recharge period, and is evidence of soil acting as a capacitor of moisture by storing winter precipitation for growth later (Bisigato et al. 2013).

Water need and immediate use

Whereas the average antecedent stored SM was important early in the growing season, by July SM did not occur in competitive models for either grassland. At this time other measures of water availability and use became more important predictors. Although not always the top predictor, D was important June through September in the grazed grassland and July through September in the ungrazed grassland. The importance of D in June through September models suggested that plant response in times of minimal SM was affected by water need (D) as well as availability (AET or P). Sensitivity to D rather than water availability or use was consistent with a drought response noted by Munson et al. (2013) and Vicente-Serrano et al. (2013), who described the importance of drought duration and severity on semi-arid vegetation. Response to P and AET rather than SM at this time of year indicates some monsoon precipitation was used immediately. Notaro et al. (2010) described the same sequence and timing of events across the entire monsoon region of North America.

Monsoon NDVI response

The inter-annual variation in moisture availability late in the growing season was reflected in a double or single peak in the annual NDVI curves. This bimodal NDVI response is ascribed to depletion of stored SM in March–May followed by a pre-monsoon drought in June with renewed vegetation growth if monsoon precipitation occurs (Notaro et al. 2010). In July through October, a near-term NDVI response to AET and P was found in both grasslands. This time of year AET and P in response models represents immediate use of P such that it does not add appreciably to SM until October (Appendix S1). In October and November, SM averaged across the preceding growing season was the most frequent predictor in response models for both grasslands suggesting end of season NDVI response is primarily due to sustained levels of growing season SM.

Functional NDVI response differences

The temporal correlation in NDVI for the two grasslands suggests they respond similarly to climatic conditions, but lack of perfect agreement also suggests different response mechanisms. We found differences in vegetation composition and abundance that explain patterns in grassland phenology (Epstein et al. 1999; Reynolds et al. 2004; Fabricante et al. 2009; Moreno-de las Heras et al. 2015).

The higher productivity in the ungrazed grassland was mostly due to higher annual precipitation, more vegetation cover and perhaps partially due to higher species richness that enables access to water in more temporal niches and soil profile depths (Muldavin et al. 2008; Notaro et al. 2010; Moreno-de las Heras et al. 2015). In the grazed grassland, there was less C_3 grass cover, lower species richness and more unpalatable species, which is consistent with the effects of grazing in this region (Fleischner 1994; Rosenstock 1996; Harris et al. 2003) and which likely influenced the NDVI responses to climate and water balance.

Although it was not the most frequent predictor, there was evidence that GDD in March was correlated with April vegetation greenness in the ungrazed grassland, a finding supported by others where C_3 species occur in grasslands of the Chihuahuan Desert (Muldavin et al. 2008; Notaro et al. 2010). This was consistent with higher cover of C_3 'cool season' species in ground plots in the ungrazed grassland, and mostly C_4 'warm season' grasses in the grazed grassland. Evidence of a more rapid green-up in the ungrazed grassland was found in the higher rate of NDVI change in April as cool season species responded to warming temperatures (Appendix S5). Similarly, the grazed grassland maintained higher rates of growth in June–September, which was consistent with the presence of C_4 warm season species (Tieszen et al. 1997).

In the warm months April–August, we found near-term pulse response relationships where short durations and short leads were common. For example, GDD, P and AET have a short duration as available energy initiates growth and pulses of moisture and water use sustain growth, a finding consistent with those of Muldavin et al. (2008) and Notaro et al. (2010). Our early and mid-season leads agreed with others who found 1 mo lags in NDVI response and variable period length of antecedent conditions that were strongly related to plant functional type and phenological stage (Szilagyi et al. 1998; Ogle & Reynolds 2004; Reynolds et al. 2004; Notaro et al. 2010; Moreno-de las Heras et al. 2015). However, the response in our study units was as likely to result from D as from P depending on availability of incipient precipitation or strength of drought response. On the other hand, spring and autumn season responses were more commonly associated with longer durations of SM and D because NDVI in those seasons is a product of accumulated biomass affected by water availability and water stress over longer periods. These results agree with others who found that long durations of P accumulated as SM were important for spring response in semi-arid environments (Nagler et al. 2007; Jenerette et al. 2010) and as shown here for end of season response.

Precipitation legacies and pulse reserve

The pulse reserve concept describes how biological reserves limit vegetation response in successive seasons based on root, stem and seed biomass that respond to growing conditions in following years (Lauenroth & Sala 1992; Reynolds et al. 2004). This concept explains the poor relationships between annual above-ground net primary productivity (ANPP) and annual P even when spatial patterns of ANPP with P are very strong globally (Sala et al. 2012). We found a weak positive relationship between i NDVI and annual precipitation ($r^2 = 0.24$ ungrazed and $r^2 = 0.05$ grazed) that was much stronger when i NDVI lagged annual P by 1 yr ($r^2 = 0.52$ ungrazed and $r^2 = 0.41$ grazed). Evidence of the pulse reserve concept was also apparent in durations >1 yr. Productivity cycles, especially of grasses, are partially dependent on biological reserves from prior years and are important factors that can be overlooked or under-appreciated unless careful accounting of cumulative effects and frequent observations are part of the monitoring and management strategy (Sala et al. 2012).

Dynamic monitoring for dynamic management

Consideration of flexible windows of relevant antecedent conditions rather than focusing on precipitation average or deviation from average can improve understanding of semi-arid vegetation response (Easdale & Bruzzone 2015). Attention to unique response windows of different plant functional types is also important (Vicente-Serrano et al. 2013). Our study confirms these points and further demonstrates that there can be seasonal switches in the best climate and water balance variables and their corresponding antecedent influence on different vegetation assemblages (Reynolds et al. 2004; Robinson et al. 2012). Others point out that seasonal precipitation is more important than annual precipitation in its control on ANPP (Robinson et al. 2012) and also note the important effect of soil properties that facilitate storage and distribution to deeper layers (Munson et al. 2011, 2013; Bisigato et al. 2013). Our emphasis on monthly aspects of water availability and vegetation response helped identify seasonality in drivers (e.g. switches between moisture availability and deficit), temporal windows of importance (e.g. SM recharge over cool season) and inter-annual patterns that result from precipitation legacies (pulse reserve relationships). These findings confirm complex relationships between climate, landscape physical factors, land use and vegetation types, but importantly provide a means to interpret these relationships in ways that can improve our understanding and management of grasslands. Semi-arid

landscapes are dynamic and our monitoring and management actions should reflect variation in the spatial and temporal state of vegetation.

Forecasts

Our multi-model forecasts allowed the predictor variables and associated antecedent windows to vary by grassland and month, relying more on high-ranked models that had the most support in the data. The multi-model forecasts performed better than a naïve NDVI climatology forecast, which confirms that our models contain information pertinent to NDVI response. In the 100 iterations used to make the forecast, accuracy was generally high in average precipitation or dry years and was less accurate when there were consecutive above average precipitation years. This was likely due to complexities associated with pulse reserve relationships that are challenging to our model built with a 14-yr time series. Forecast accuracy was similar across 3 yrs for both grazed and ungrazed grasslands, and the response models generally predicted higher NDVI in the ungrazed grassland each year. Improvements in forecasting could come from better accounting of pulse reserve influences, stocking rates or forage utilization in the grazed grassland, and employing a longer record of measurements.

The significance of identifying different climate and water balance windows to explain vegetation greenness is that they all can provide sound predictions to inform management. For instance, the grazed grassland in our study was grazed from October to March. Predictive models of vegetation greenness with up to 4 mo lead time could be useful in planning stocking rates, which was also noted by Fabricante et al. (2009). Our monthly vegetation response models represent an improvement over interpretations that could be made from sampling intervals that span several years, during which both increases and decreases in greenness may occur (Munson et al. 2011).

Conclusions

Vegetation response to climate and water balance on monthly time scales is complex, but high frequency monitoring via remote sensing provides a means to determine response across broad or remote areas where traditional ground-based monitoring is not practical. If strong relationships can be developed at management scales, near-term forecasts of vegetation condition are possible simply from tracking weather and water balance. Building an operational near-term forecasting system will require development of site-specific relationships because the response is governed by complex spatially varying factors

including land use, vegetation assemblage and local climate.

We found strong relationships between climate, water balance factors and monthly NDVI that produced reasonably accurate monthly forecasts of NDVI for three holdout years. Importantly, we identified vegetation response lags up to several months that provide early warning or lead time for potential management response. Our approach relied on explicit consideration of vegetation composition and land management, lagged vegetation response and windows of time during which climate and water balance influenced NDVI. This approach provides powerful insight to potential climate-induced vegetation change that can be monitored with remote sensing, a conclusion also noted by Moreno-de las Heras et al. (2015). Our approach relied on a probabilistic representation of explanatory variable importance that did not require *a priori* knowledge of ecosystem function, which is more complex and elusive than generally acknowledged (Sala et al. 2012; Robinson et al. 2012). This approach considers that a single best model is unlikely to emerge and that multiple factors simultaneously play important roles in determining vegetation condition (Burnham & Anderson 2002). Water balance proved to be useful for assessing vegetation response beyond climate alone in most months because it incorporated estimates of water availability, use and unmet vegetation need.

Knowing where in the pulse reserve cycle semi-arid vegetation is currently and how vegetation may respond to wet or dry conditions in upcoming seasons can provide insight to potential response. This, in turn, may help with decisions regarding stocking rates or help with planning for restoration activities that should be timed during optimal growing conditions. Better understanding of drought effects, including local resistance and resilience to water deficits, are important considerations for management (Vicente-Serrano et al. 2013). Our findings contribute to the suite of information managers can use for near-term actions that set the course to achieve long-term management goals.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Monthly variation in NDVI, climate and water balance variables (2000–2013) used to model vegetation response.

Appendix S2. Best monthly model ($\Delta AIC_c = 0$) from monthly pools of competitive models with holdout years 2001, 2005, 2010.

Appendix S3. Cumulative mean forecast accuracy from k-fold validation procedure for 100 iterations.

Appendix S4. Observed vs multi-model forecast with 1:1 line and month labels for holdout years 2001, 2005, 2010.

Appendix S5. Average monthly rate of change in $NDVI \pm SE$.