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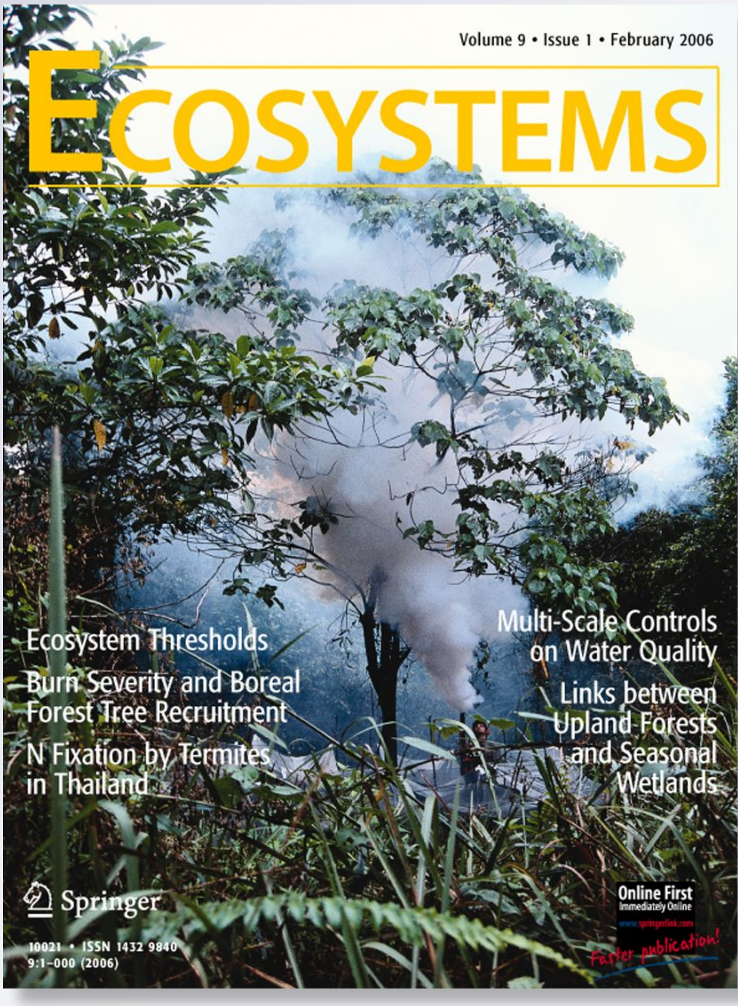

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Spatiotemporal Patterns of Production Can Be Used to Detect State Change Across an Arid Landscape

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Abstract

Methods to detect and quantify shifts in the state of ecosystems are increasingly important as global change drivers push more systems toward thresholds of change. Temporal relationships between precipitation and aboveground net primary production (ANPP) have been studied extensively in arid and semiarid ecosystems, but rarely has spatial variation in these relationships been investigated at a landscape scale, and rarely has such information been viewed as a resource for mapping the distribution of different ecological states. We examined the broad-scale effects of a shift from grassland to shrubland states on spatiotemporal patterns of remotely sensed ANPP proxies in the northern Chihuahuan Desert. We found that the normalized difference vegetation index (NDVI), when averaged across an eight-year period, did not vary significantly between these states, despite changes in ecosystem attributes likely to influence water availability to plants. In contrast, temporal relationships between precipitation and time-integrated NDVI (NDVI-I) modeled on a per-pixel basis were sensitive to spatial variation in shrub canopy cover, a key attribute differentiating ecological states in the region. The slope of the relationship between annual NDVI-I and 2-year cumulative precipitation was negatively related to, and accounted for 71% of variation in, shrub canopy cover estimated at validation sites using high spatial resolution satellite imagery. These results suggest that remote sensing studies of temporal precipitation–NDVI relationships may be useful for deriving shrub canopy cover estimates in the region, as well as for mapping other ecological state changes characterized by shifts in long-term ANPP, plant functional type dominance, or both.

Key words: aboveground net primary production; normalized difference vegetation index; precipitation; remote sensing; Chihuahuan Desert; state change; shrub encroachment; grassland; shrubland.

Introduction

Ecological state change driven by human activities is commonly reported in terrestrial ecosystems (Archer and others 1995; Ares and others 2003; Firn and others 2010; Kéfi and others 2007). Applied to rangelands, the ecological state concept is meant to differentiate areas having similar ecological potential based on climate, soils, topography, and

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proximity but different vegetation dynamics or long-term productivity due to persistent (and often human-induced) changes in certain biophysical attributes (Bestelmeyer and others 2009). Examples of such biophysical changes include truncation of surface soil horizons (Schlesinger and others 1990), development of recruitment limitations for desirable plant species (Standish and others 2007), and changes in wildfire susceptibility and frequency (Knapp 1996). Information about the geographic distribution of ecological states can help guide land management and policy, yet spatially explicit data are often lacking or incomplete.

Remote sensing has long been used to supplement and scale field observations and other localized data. Correlations between aboveground net primary production (ANPP) and remotely sensed vegetation indices such as the normalized difference vegetation index (NDVI) have enabled anthropogenic impacts on ANPP to be studied at broad spatial scales (Box and others 1989; Paruelo and others 1997, 2000; Prince 1991). In arid and semiarid ecosystems, where precipitation variability is often high and ANPP and precipitation are often coupled, many remote sensing studies have utilized precipitation use efficiency, or ANPP per unit precipitation, as a means of monitoring directional changes in ANPP not associated with climate (Holm and others 2003; Nicholson and others 1998; Prince and others 1998). Given the same amount of precipitation, sites with diminished soil quality and resource retention are expected to be less productive than non-degraded sites with similar climatic, topographic, and soil characteristics. Although this approach may be useful for mapping and monitoring human-induced landscape transformations characterized by declining productivity, it may fail to distinguish among ecological states exhibiting little difference in long-term ANPP.

The replacement of perennial grasslands with shrublands in the northern Chihuahuan Desert is an example of an ecological state change having considerable impact on ecosystem services but potentially negligible effects on landscape scale ANPP (Gibbens and others 2005). A combination of factors, including livestock grazing and severe drought, likely initiated localized shifts from grass to shrub dominance during the past century (Havstad and Schlesinger 2006). Subsequent changes in soil nutrient distribution, erosion rates, microclimate, and faunal populations have resulted in feedback loops that have accelerated and maintained the transition to a shrubland state (d'Odorico and others 2010; Eldridge and others 2009; Schlesinger and others 1990). Because of declining soil quality and increased runoff at patch to landscape scales, it is often assumed that sites dominated by shrubs are less efficient than grasslands at converting precipitation into ANPP (Huenneke and Schlesinger 2006). Long-term ANPP of grass and shrub-dominated communities measured on similar soils is not, however, remarkably different (Huenneke and others 2002; Muldavin and others 2008; Peters and others 2011). Thus, although shrub expansion in the northern Chihuahuan Desert may be undesirable for various reasons (Krogh and others 2002; Li and others 2007), it appears to have little consequence for ecosystem ANPP.

The growing inventory of high temporal resolution satellite imagery continues to open new possibilities for extracting ecological information from remotely sensed time series. One remote sensing approach with the potential to detect geographic variation in both long-term ANPP and plant functional type dominance in water limited systems is the study of temporal ANPP responses to inter-annual precipitation fluctuations (Verón and others 2006). Combining satellite imagery with spatially continuous precipitation estimates allows temporal relationships between precipitation and remotely sensed ANPP proxies to be statistically modeled on a pixel-by-pixel basis. The marginal mean of these regressions provides a measure of temporally averaged ANPP that should be largely independent of spatial rainfall variability. In addition, such relationships may prove useful for studying vegetation composition, due to plant morphological and physiological trade-offs that influence regression parameters such as slope, intercept, and coefficient of determination (Omuto and others 2010; Verón and Paruelo 2010).

Plant traits facilitating rapid biomass production during favorable conditions, for example, are often associated with relatively low drought tolerance and short life spans (Chapin 1993; Grime 1977). Such traits are common among grass and forb species of the northern Chihuahuan Desert. In contrast, long-lived species such as shrubs allocate resources to structural tissue and defenses, often at the expense of low relative growth rates. Between these contrasting groups, ANPP of shorter lived functional types is expected to more closely track inter-annual precipitation and display a higher rate of change (Peters and others 2011). Thus, even if remotely sensed ANPP proxies are similar between sites dominated by different functional types over the long term, the relationship of these proxies to inter-annual rainfall fluctuations presents a potentially useful trait for mapping plant functional type dominance across broad scales (Bradley and Mustard 2005; Verón and Paruelo 2010).

Addressing the need for remote sensing methods applicable to a variety of terrestrial state changes, we examined the impact of state change on spatiotemporal patterns of ANPP in the northern Chihuahuan Desert of New Mexico, USA using remotely sensed data. We assembled a time series of satellite imagery and interpolated precipitation estimates for a landscape where variations in land-use history have led to strong gradients in shrub and perennial grass dominance on similar soils (Gibbens and others 2005). Our first objective was to assess if remotely sensed proxies of ANPP, when averaged over time, vary consistently across these vegetation gradients. Although localized monitoring in the region suggests little difference in long-term ANPP between grassland and shrubland sites occurring on similar soils (Peters and others 2011), we sought to test if such patterns hold true at a landscape scale when examined using satellite data. A second objective was to examine if grass and shrub-dominated sites differ in their NDVI response to inter-annual precipitation variation. Such differences are plausible considering the contrasting functional traits of herbaceous and woody species, yet they have not been well documented at a broad scale.

The analyses presented here aim to improve understanding of vegetation dynamics in the region. They also aim to improve the mapping and monitoring of ecological states at spatial scales relevant to land management and policy. If ecological states consistently differ in either long-term ANPP or temporal ANPP variability, as measured using remotely sensed data, then such differences should enable better estimates of the geographic distribution of these states. Here, we apply this approach to a state change involving replacement of perennial grasses with shrubs.

Methods

General Approach

To study variation in (1) long-term average NDVI and (2) precipitation–NDVI relationships across gradients of woody and herbaceous plant cover, we paired an eight-year (2002–2009) time series of MODIS NDVI with gauge-based precipitation estimates. Temporal relationships between time-integrated NDVI (NDVI-I) and select precipitation metrics were modeled on a per-pixel basis using simple linear regression (Wessels and others 2007). The slope (hereafter referred to as Precipitation Marginal Response, or PMR, following Verón and others 2005), coefficient of determination, and marginal mean of these regressions were then analyzed against herbaceous foliar cover estimated in the field and shrub canopy cover extracted from high spatial resolution satellite imagery. The analysis followed four steps. We (1) studied the effectiveness of various precipitation metrics at explaining year-to-year variation in annual and seasonal NDVI-I for the study landscape as a whole, (2) examined the sensitivity of these relationships and mean annual NDVI-I to spatial variation in woody and herbaceous cover, (3) assessed the strength of ANPP-NDVI-I correlations at long-term monitoring sites embedded within the study landscape, and (4) investigated the utility of temporal precipitation–NDVI-I regressions for mapping ecological states dominated by different plant functional types.

Study Area

The study landscape included adjacent portions of the USDA Jornada Experimental Range and the Chihuahuan Desert Rangeland Research Center. These research facilities lie at the southern end of the Jornada Basin of southern New Mexico, USA (latitude 32°37′15″, longitude −106°44′14″) and encompass the Jornada Basin Long Term Ecological Research site (http://jornada-www.nmsu.edu). Climate is arid to semiarid, with long-term (90 years) mean annual temperature of 15°C and mean annual precipitation of 250 mm, nearly all of which occurs as rain. On average around 54% of annual precipitation occurs during the summer (July–September), about 21% in the fall (October–December), and the remaining approximately 25% in the winter and spring (January–June). This study spanned a period of unusually variable precipitation (Figure 1). Annual rainfall in 2003 was about half the long-term average, whereas 2006 rainfall was near record highs. Precipitation is also spatially variable in the region due to summer convective storms that produce intense localized rainfall. To account for this variability, the study landscape was limited to an area bounded by the extent of low elevation rain gauges plus a buffer of about 2 km. Coverage of available high resolution satellite imagery further constrained the area to approximately 525 km^2. Slopes are mostly less than 3 percent grade, and livestock grazing occurs at low intensities.

Precipitation Interpolation

In assessing temporal relationships between NDVI-I and precipitation, several different dependent and independent variable combinations were considered (Table 1). Annual and seasonal scales were both

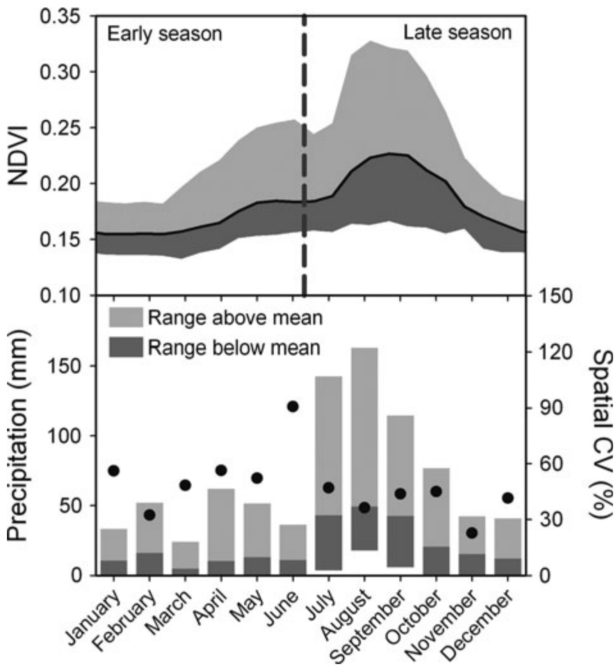

Figure 1. Annual NDVI and precipitation profiles for the study area. NDVI mean and range were calculated for each 16-day compositing period using average study area NDVI from 2002 to 2009. Monthly precipitation statistics were calculated using the average of 41 rain gauges from 2001 to 2009. *Round symbols* indicate the average monthly coefficient of variation (CV) among rain gauges during this period.

included in the analysis, and 2-year cumulative precipitation was used as an explanatory variable to address lagged precipitation effects on NDVI-I (Oesterheld and others 2001). We focused on straightforward precipitation metrics and did not attempt to examine all possible variable combinations. Gridded precipitation surfaces were created using monthly data from 52 standard collecting rain gauges summed to seasonal or annual totals (11 gauges lay outside the study area boundary). Trends at monthly intervals were not studied because of differences in gauge visitation dates and because dominant shrub species exhibit seasonal phenology largely unrelated to precipitation amount and timing (Reynolds and others 1999). Precipitation surfaces were produced using natural neighbor interpolation (Esri 2010). Interpolation artifacts arising near the edges of the surfaces were avoided by arranging dummy points along the periphery of the gauge network and assigning these points precipitation estimates derived from Nexrad radar. More complex interpolation methods (for example, kriging) were not warranted given the area's simple topography and low relief.

Image Processing

We acquired, merged, and subset MODIS 250 m resolution vegetation indices datasets for the area and time frame of interest. These datasets were obtained from the USGS Land Processes Distributed Active Archive Center as a 16-day composite product (MOD13Q1). The compositing procedure essentially creates a mosaic image of the ''best'' NDVI measurements collected during each 16-day period, thereby reducing NDVI anomalies associated with cloud cover and low sensor view angles (Huete and others 2002). We screened the data further by replacing NDVI values associated with a rank of 2 (snow/ice) or 3 (cloudy) in the MOD13Q1 pixel reliability layer with a moving average calculated from the two preceding and two subsequent periods in the time series. Values more than 100% above or 40% below both the average of the two preceding periods and the average of the two subsequent periods were replaced in the same fashion. Less than 0.001% of pixels in our study area required replacement.

We followed a common practice of using time-integrated NDVI (NDVI-I) as a proxy for ANPP (Box

Table 1. Temporal Precipitation–NDVI-I Regression Models Examined in the Study

Dependent NDVI-I variable	Explanatory precipitation variable	Study area summary statistics	
		Mean r^2	Proportion $P < 0.05$
Annual	Current year	0.15	0.01
Annual	Previous year	0.45	0.42
Annual	2 year	0.65	0.80
Early season	Fall-winter	0.46	0.39
Early season	Previous summer	0.58	0.71
Early season	Summer-fall-winter	0.82	0.99
Late season	Summer	0.56	0.63

Summary statistics are based on the population of pixels within the study area.

and others 1989; Holm and others 2003; Paruelo and others 1997; Wessels and others 2007). A consistent NDVI minimum was observed near the beginning of each calendar year, at a time when foliar biomass of herbaceous and woody deciduous species has typically become senescent (Figure 1). This winter minimum indicated a natural break in plant photosynthetic activity and led us to select annual NDVI-I, calculated on a per-pixel basis by summing the 23 composite values for a single calendar year, as a dependent variable in precipitation–NDVI-I regressions (Table 1). The NDVI sum from day-of-year (DOY) 177 through day 3 or 4 of the following year (late season NDVI-I) was independently considered as a dependent variable because C4 grass production is highest during the summer and fall (Huenneke and others 2002; Muldavin and others 2008). Spring production by annuals and C3 shrubs was addressed using total NDVI from DOY 1 through DOY 176 (early season NDVI-I). Each sum was divided by 23 to report NDVI-I values on the more familiar −1 to 1 NDVI scale.

Field Validation

Three basic outputs of the pixel-based regressions [the coefficient of determination (r^2), slope (PMR), and P value of the slope] were mapped back to the MODIS grid for visual interpretation. Regression marginal means were also derived on a per-pixel basis by first determining the mean value of each precipitation metric for the study area and time period and then inserting these values into the associated regression equations. Visual assessment of the resulting maps was supplemented with field data collected at the approximate centroid of 59 MODIS grid cells randomly selected from the population of cells not intersected by well traveled roads. Within a 20 × 20 m plot, visual estimates of foliar cover were recorded for all perennial plant species contributing more than 1% cover. To address soil differences among sites, soils were sampled to a depth of 100 cm (or depth to a restrictive horizon) using a 6 cm diameter auger. Each plot was subsequently assigned to a US Natural Resources Conservation Service ecological site class, which stratify the landscape based on differences in soil profile characteristics and topographic position that affect primary productivity and potential plant species composition (Bestelmeyer and others 2009). Plots fell predominantly on sandy (26 plots) and shallow sandy (15 plots) ecological sites, with five other ecological site classes also represented (Figure 2).

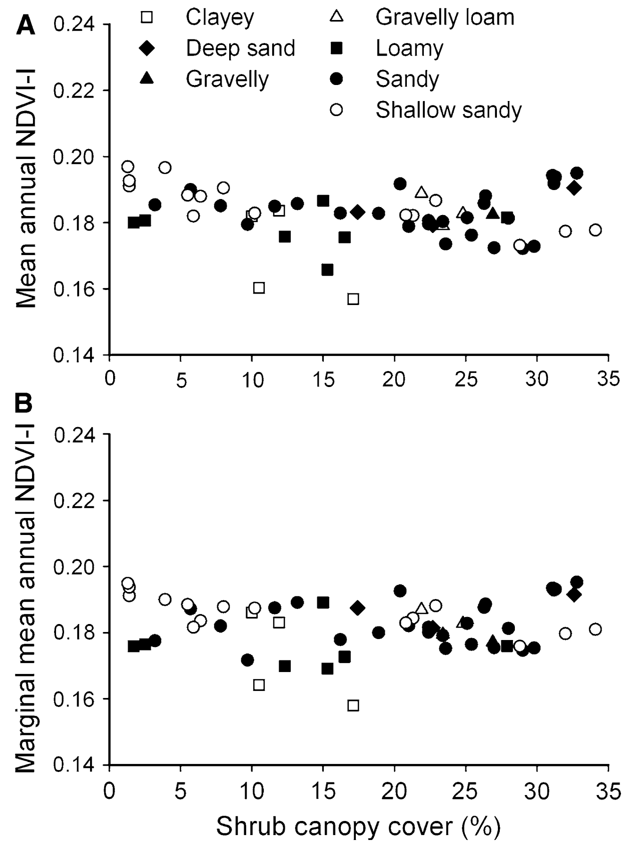

Figure 2. **A** Mean annual NDVI-I and **B** marginal mean annual NDVI-I at 59 randomly located validation sites from 2002 to 2009. Marginal mean annual NDVI-I was calculated on a per-pixel basis by inserting average 2-year cumulative rainfall for the study area and time period (514 mm) into the regression equations predicting annual NDVI-I from 2-year cumulative precipitation. $N = 4, 3, 1, 3, 7, 26,$ and 15 for clayey, deep sand, gravelly, gravelly loam, loamy, sandy, and shallow sandy ecological sites, respectively.

Because of the areal discrepancy between field plots (20 m) and MODIS grid cells (~230 m), shrub canopy cover was estimated for entire cells using 60 cm resolution panchromatic QuickBird imagery (DigitalGlobe 2006). In locations with low perennial grass cover, high contrast between shrub crowns and the surrounding soil, litter, and vegetation allowed large shrubs (>~1 m) to be efficiently classified using brightness value thresholds. Performance of the method was enhanced by first calculating the difference between each pixel value and the mean of a surrounding 17 or 33-cell diameter circular neighborhood. This operation accentuated small, dark shrub canopies while subduing large, dark perennial grass patches, thereby improving shrub classification in areas with dense perennial grass cover. Threshold values were iteratively applied to the resulting index until a balance between errors of omission and commission, as visually apparent from the original imagery, was achieved. This process was applied to image subsets covering each randomly selected grid cell. Average shrub cover was subsequently computed within an area covered by each grid cell plus a 58 m (~1/4 grid cell width) buffer. Imagery acquired by QuickBird in May 2003 was used to estimate shrub canopy cover at all but seven validation sites, with imagery from September 2003 or May 2006 substituted in areas of insufficient coverage. Simple linear regression was used to analyze trends between vegetation cover estimates and precipitation–NDVI-I regression parameters.

We also compared repeated measures of NDVI-I and ANPP at long-term sites within the study area monitored since 1990. This monitoring network consists of fifteen sites representing five dominant vegetation types in the Chihuahuan Desert: grassland, mesquite shrubland, creosotebush shrubland, playa, and tarbush. All sites consist of 48 or 49 1-m^2 sample quadrats spaced at 10 m intervals within an area excluded from livestock. Average ANPP at each site was estimated for three seasons (spring, summer-fall and winter) using a non-destructive volumetric approach described by Huenneke and others (2001) and revised by Peters and others (2011). For all vegetation types except playa and mesquite shrubland, we selected two sites that appeared most suitable for comparison with coarse resolution satellite imagery. A 2 × 2 pixel footprint was chosen that intersected or was less than one pixel from each plot and was most representative of conditions found within that site. Playa sites were not included in the analysis because the 2 × 2 pixel footprint was too large in most cases. Mesquite shrubland sites were excluded because allometric equations requiring adjustment following recent reference harvests were unavailable. The selected footprints inevitably included landscape features not present within ANPP plots, including dirt roads.

For 2002 through 2009, temporal relationships between field-estimated ANPP and average NDVI-I of the four corresponding MODIS cells were assessed using linear mixed models (PROC MIXED, SAS Institute 2008). Separate models were constructed to predict annual, early season, and late season NDVI-I using annual, spring, and summer-fall ANPP, respectively. One set of models was designed to account for potential differences in NDVI-I among sites, because soils and other geomorphic characteristics are known to influence the NDVI and may vary even among sites having similar vegetation. ANPP, site, and their interaction constituted the explanatory terms of these models. Another set was constructed to assess NDVI-I differences among vegetation types, and these included ANPP, vegetation type, and their interaction as fixed effects. Site and its interaction with ANPP were included as random effects in the latter set to account for additional correlation among model residuals of repeated observations. All statistical tests used a significance level of 5%.

Results

Precipitation–NDVI-I Relationships

Annual and seasonal NDVI-I were both related to inter-annual precipitation variation during the time frame of the study. Not surprisingly, the average coefficient of determination of pixel-based regressions, when computed for the study area as a whole, depended on the NDVI-I and precipitation metrics used (Table 1). Two-year cumulative precipitation emerged as the metric explaining the greatest amount of temporal variation in annual NDVI-I (r^2 = 0.65). Considerably poorer performance was exhibited, on average, by pixel-based regressions using annual NDVI-I as the dependent variable and only current year (r^2 = 0.15) or previous year precipitation (r^2 = 0.45) as the explanatory variable. On average, summer rainfall (July–September) explained 56% of the variation in late season NDVI-I measured the same year and 58% of the variation in early season NDVI-I the following year. Fall-winter precipitation (October–March) explained 46% of variation in early season NDVI-I on average. Adding previous summer precipitation to fall and winter totals improved the fit with early season NDVI-I (r^2 = 0.82).

Mean and Marginal Mean NDVI

Shrub canopy cover at validation sites ranged from 1 to 34%, and these estimates were unrelated to eight-year (2002–2009) mean annual NDVI-I of the corresponding MODIS pixels (Figure 2). An analysis of regression marginal means yielded similar results. Only when summer precipitation was used to predict late season NDVI-I did the marginal mean show a significant negative relationship to shrub canopy cover (r^2 = 0.10; Table 2). The marginal mean of models used to predict early season NDVI-I exhibited a significant negative relationship to herbaceous foliar cover in all cases, but the marginal mean of models used to predict annual or late season NDVI-I was unrelated to this vegetation attribute.

Table 2. Relationship of Precipitation–NDVI-I Regression Parameters to Shrub and Herbaceous Cover

Dependent NDVI-I variable	Explanatory precipitation variable	Relationship of precipitation–NDVI-I regression parameters to shrub canopy cover						Relationship of precipitation–NDVI-I regression parameters to herbaceous foliar cover					
		R^2		PMR		Marginal mean		R^2		PMR		Marginal mean	
		R^2	Sign	R^2	Sign	R^2	Sign	R^2	Sign	R^2	Sign	R^2	Sign
Annual	Current year	0.56	–	0.66	–	0.02	NS	0.29	+	0.30	+	0.02	NS
Annual	Previous year	0.25	+	0.12	–	0.01	NS	0.32	–	0.01	NS	0.03	NS
Annual	2 year	0.51	–	0.71	–	0.00	NS	0.26	+	0.30	+	0.05	NS
Early season	Fall-winter	0.00	NS	0.33	–	0.04	NS	0.05	NS	0.01	NS	0.27	–
Early season	Previous summer	0.00	NS	0.42	–	0.06	NS	0.00	NS	0.09	+	0.30	–
Early season	Summer-fall-winter	0.00	NS	0.58	–	0.07	NS	0.00	NS	0.09	+	0.30	–
Late season	Summer	0.59	–	0.72	–	0.10	–	0.34	+	0.33	+	0.02	NS

Simple regression was used to evaluate relationships between precipitation–NDVI-I regression parameters and either shrub canopy cover estimated from high resolution satellite imagery or herbaceous foliar cover visually estimated at 20 × 20 m field plots. NS indicates a slope not significantly different from zero at the 5% level.
Summer = July–September, fall = October–December, and winter = January–March.

Sensitivity of Precipitation–NDVI-I Regressions to Vegetation Composition

In contrast to mean and marginal mean NDVI, temporal NDVI-I responses to precipitation fluctuations were clearly sensitive to spatial variation in shrub canopy cover (Table 2). This sensitivity surfaced in the coefficient of determination and slope of individual pixel-based regressions. Shrub canopy cover estimated from high spatial resolution satellite imagery was used to assess the response of regression parameters to variable shrub dominance at validation sites. These data indicated that r^2 values tended to decline with increasing shrub cover when current year precipitation was used as the explanatory variable and increase when previous year precipitation was used. For the majority of pixels, however, the slopes of these precipitation–NDVI-I regressions were not significantly different from zero (Table 1). A considerably larger proportion of pixels had statistically significant slopes when either 2-year cumulative precipitation (0.80) or summer rainfall (0.63) was used as the explanatory variable. In these cases, r^2 values generally declined as a function of increasing shrub canopy cover (Table 2). No significant relationships were observed between shrub canopy cover and r^2 values of the precipitation–NDVI models used to predict early season NDVI-I.

Regression slope, or PMR, was in general more strongly related to shrub canopy cover than was the coefficient of determination (Table 2). This was particularly true when either 2-year cumulative precipitation ($r^2 = 0.71$) or summer rainfall ($r^2 = 0.72$) was used as the explanatory variable in precipitation–NDVI-I regressions (Figure 3). PMR declined with increasing shrub canopy cover no matter which variable combinations were used. The contrasting sensitivities of PMR and marginal mean NDVI-I to shrub cover variation reflect the fact that sites with high PMR also tended to have low regression y-intercepts, and vice versa. Thus, for the ecosystem attributes studied here, the slope and y-intercept of precipitation–NDVI-I regressions generally provided similar information.

Visual estimates of species foliar cover at field sites were used to assess the sensitivity of precipitation–NDVI-I regression parameters to spatial variation in perennial herbaceous cover. For five of the precipitation and NDVI-I variable combinations examined, total herbaceous foliar cover on 20 × 20 m plots exhibited a weak but significant positive relationship to PMR (Table 2). Nevertheless, multivariate regressions using both field estimates of herbaceous foliar cover and remotely sensed estimates of shrub canopy cover as explanatory variables were able to account for only slightly more variance in PMR compared to when shrub canopy cover was used alone (data not shown). Plotting herbaceous foliar cover as a function of shrub canopy cover suggested an upper limit to herbaceous cover in this ecosystem as shrub cover increases (Figure 4). It is unlikely that variation in PMR can be attributed to differences in total plant cover, because total foliar cover (herbaceous, sub-shrub, and shrub) estimated at field plots was not significantly related to either PMR or shrub canopy cover (data not shown).

Correlations Between NDVI-I and ANPP

Long-term ANPP monitoring data verified that NDVI-I provides a reasonable proxy for ANPP at individual Chihuahuan Desert sites through time. A total of 84% of the variation in annual NDVI-I repeatedly measured at monitoring sites was explained by a linear model whose main effects were annual ANPP, site, and their interaction (Figure 5). Of these three effects, only annual ANPP was statistically significant ($P < 0.001$). Spring and summer-fall ANPP were the only significant effects in equivalent models used to predict early season and late season NDVI-I, respectively. These models accounted for 50% of early season and 91% of late season NDVI-I variation. When included as model variables, neither vegetation type nor its interaction with ANPP had a significant effect on annual, early season, or late season NDVI-I. Thus, for all of the models considered, ANPP was the only variable successful at explaining NDVI-I variation though space and time.

Mapping Plant Life Form Cover

As noted above, the relationship between annual NDVI-I and 2-year cumulative rainfall was statistically significant at 80% of pixels within the study area. Shrub canopy cover was also a strong predictor of the slope of this relationship. Transposing independent and dependent variables, we found that PMR based on annual NDVI-I and 2-year cumulative rainfall accounted for 71% of shrub canopy cover variation and 30% of herbaceous foliar cover variation among validation sites (Table 2), which suggests that shrub cover can be reasonably estimated from PMR in this region (Figure 6). Prediction intervals indicated that 95% of the time the difference between shrub canopy cover predicted by PMR and values obtained using high resolution satellite imagery was expected to be less than about 11% cover (Figure 3). Individual predictions of herbaceous cover at the pixel scale were expected to differ from ground truth values by less than about 27% cover 95% of the time.

Discussion

Precipitation–NDVI-I Relationships

Temporal ANPP variation is related to year-to-year precipitation fluctuations in many terrestrial systems (Huxman and others 2004; Smoliak 1986).

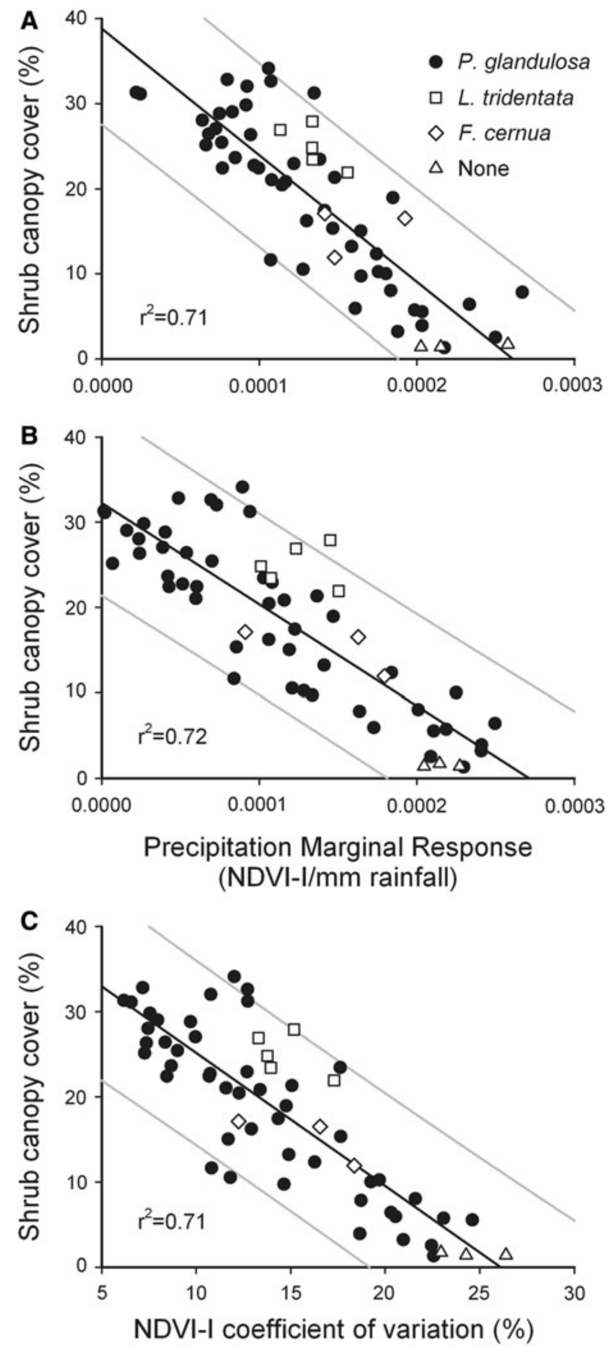

Figure 3. Inter-annual NDVI-I response variables useful for predicting shrub canopy cover. Panels show trends in shrub canopy cover remotely estimated at validation sites as a function of **A** the slope of the temporal relationship between annual NDVI-I and 2-year cumulative precipitation, **B** the slope of the temporal relationship between late season NDVI-I and summer precipitation, and **C** the late season NDVI-I coefficient of variation from 2002 to 2009. *Symbols* indicate the dominant shrub species based on foliar cover visually estimated in the field. *Prosopis glandulosa* and *Flourensia cernua* are winter deciduous species, whereas *Larrea tridentata* is evergreen. The 95% prediction intervals are shown in medium *gray*.

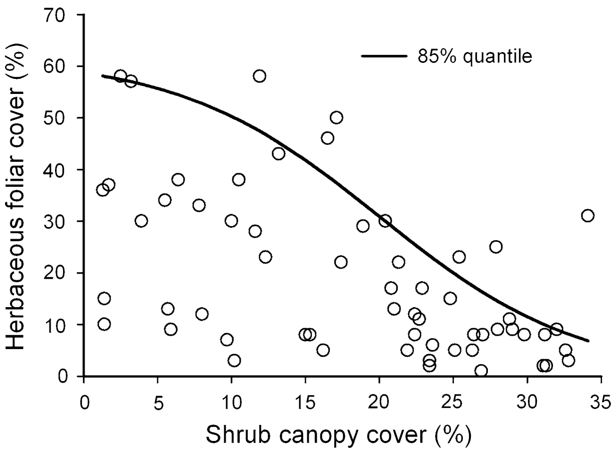

Figure 4. Relationship between visually estimated herbaceous foliar cover at validation sites and shrub canopy cover estimated from 60 cm resolution satellite imagery. The 85th quantile logistic curve was derived using quantile regression.

There is little consensus among studies, however, as to how much ANPP variance at individual sites can be attributed to temporal changes in annual precipitation (Le Houérou and others 1988). In the northern Chihuahuan Desert, Huenneke and others (2002) reported poor associations between annual rainfall and annual ANPP from 1990 to 1998. More recent analyses of this expanding dataset show that predictions can be improved by distinguishing sequences of dry and wet years (Peters and others 2011). Analyzing short periods of time may also improve predictions: a six-year study in central New Mexico found annual precipitation to explain 66% of ANPP inter-annual variation at a grassland site and 56% at a nearby shrubland site (Muldavin and others 2008).

Across the eight-year period studied here, which included both extremely dry and wet years, annual rainfall was on average a poor predictor of annual NDVI-I through time at individual pixels (Table 1). Considerably more variation in annual NDVI-I was explained by precipitation occurring in the current plus previous year. Similarly, early season NDVI-I was found to strongly track total precipitation of the preceding summer, fall, and winter (July–March). This surrogate for spring ANPP was also moderately related to both total precipitation of the past summer (July–September) and total precipitation of the preceding fall and winter (October–March).

Lag effects of previous year precipitation have been noted in other studies and may involve more than just carryover of soil moisture. Oesterheld and others (2001) reported a correlation between previous and current year production in a short-grass steppe ecosystem and speculated on a host of biological mechanisms. Paulsen and Ares (1962) observed that fluctuations in grass basal area on the Jornada LTER site were most tightly coupled to precipitation of a 15 month period spanning July of the prior year through September of the current year, despite grass roots being concentrated near the surface in soils that dry out during extended drought (Duniway and others 2010; Gibbens and Lenz 2001). Annual NDVI-I in several regions of Northern Patagonia was also found to track precipitation occurring in portions of the previous year (Fabricante and others 2009). Together, these results indicate that annual precipitation may not always be the best predictor of annual ANPP in water limited systems. It appears possible for plant production in some ecosystems to respond to precipitation occurring in preceding years, to be influenced by prior droughts (Yahdjian and Sala 2006), and as highlighted in the following section, for this response to be vegetation and site

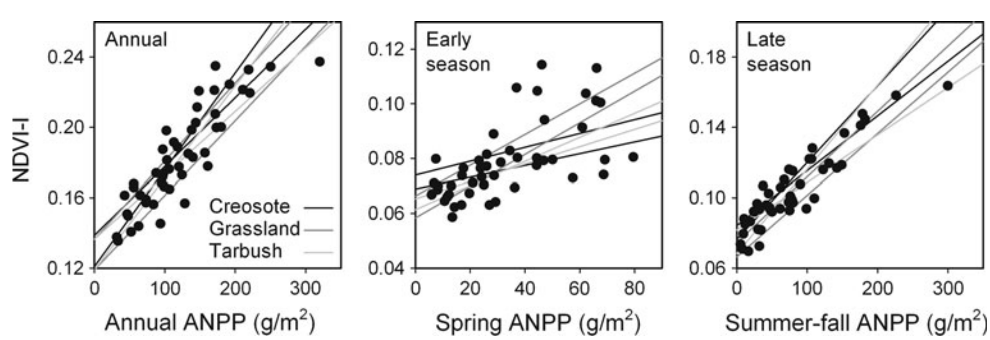

Figure 5. Relationships between ANPP and NDVI-I at six long-term monitoring sites from 2002 to 2009. Three common vegetation types in the region, creosotebush shrubland, grassland, and tarbush, were each represented by two sites. Linear models were used to predict annual, early season, and late season NDVI-I from annual, spring, and summer-fall ANPP, respectively, and included site and its interaction with ANPP as additional terms. ANPP was the only significant model effect in each case. *Lines* indicate predicted NDVI-I at each site.

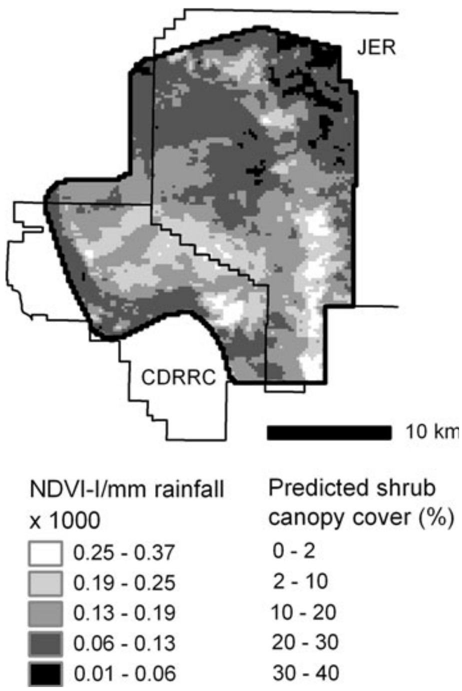

Figure 6. Spatial patterns in the slope of pixel-based regressions between annual NDVI-I and 2-year cumulative precipitation. Shrub canopy cover was estimated using the empirical relationship shown in Figure 3.

dependent. For mapping and monitoring applications, then, decisions about which precipitation and NDVI metrics to analyze may often depend on the ecosystem, species, and objectives under consideration.

Sensitivity of Precipitation–NDVI-I Regressions to Vegetation Composition

Woody plant encroachment is a phenomenon affecting large portions of the southwestern US and other arid and semiarid grasslands of the world (Archer and others 1995; Van Auken 2000). Similar to observations made at ANPP monitoring sites in the study area (Peters and others 2011), no statistical difference in mean annual NDVI-I of grassland and shrubland states was apparent across an eight-year period (Figure 2), consistent with the zero-sum model of House and others (2003). Differences did emerge, however, in the temporal NDVI-I response of individual pixels to inter-annual precipitation fluctuations. The slope of precipitation–NDVI-I regressions was negatively related to shrub canopy cover estimated from high resolution satellite imagery, regardless of the NDVI-I and precipitation variables used (Table 2).

These landscape scale trends are largely consistent with physiological and morphological trade-offs associated with woody and herbaceous plant life forms. In regions where they coexist, C3 shrubs and C4 grasses are often thought to exhibit contrasting strategies with regard to seasonal water use and biomass production (Muldavin and others 2008; Neilson 1986; Schwinning and Ehleringer 2001). C4 grass species are generally dependent on summer rainfall given their shallow root systems and physiological adaptation to growth under warm conditions (Gibbens and Lenz 2001). In contrast, deeply rooted C3 shrubs may be more dependent than grasses on precipitation occurring in the fall and winter months, when reductions in evapotranspiration can allow deep soil moisture recharge (Ehleringer and others 1991). Relative growth rates may also differ between the two life forms, with perennial grasses typically expected to translate available water more rapidly into herbaceous biomass (Chapin 1993). Moreover, at least one dominant deciduous shrub species in our study area, *Prosopis glandulosa* (honey mesquite), reliably produces spring foliage regardless of prior precipitation amounts (Reynolds and others 1999).

Given the differences noted above, it is not surprising that relationships between summer rainfall and late season NDVI-I weakened with increasing shrub canopy cover. A differential capacity of shrub and perennial grass species to capitalize on above average rainfall may also help explain why PMR generally declined as shrub canopy cover increased. Data collected at validation sites indicated a limiting relationship between shrub and herbaceous cover, suggesting that as sites become increasingly dominated by shrubs, they become less able to sustain high cover of other perennial life forms (Figure 4). Similarly, certain traits common to dominant shrubs in the region, such as extensive root systems and the ability to access more varied and potentially more reliable sources of soil moisture (Gibbens and Lenz 2001; Gile and others 1997), might be invoked to explain why PMR generally declined with increasing shrub cover while mean and marginal mean annual NDVI-I did not. In other words, certain traits may allow shrub-dominated sites to maintain higher NDVI-I during low rainfall periods than do grass-dominated sites. The variety of vegetation and soil types sampled suggests that the vegetation and/or site characteristics responsible for observed trends in NDVI-based PMR are not associated with any one dominant shrub species (Figures 2, 3). Although we focused here on vegetation, it is conceivable that abiotic changes associated with shrub encroachment, such as truncation of surface soil horizons and modification of overland water flow, might also influence PMR at the site level. Runoff, in particular, is known to increase in the northern Chihuahuan Desert with increasing shrub dominance (Neave and Abrahams 2002; Turnbull and others 2010).

Correlations Between NDVI-I and ANPP

Implicit in these ecological interpretations is the idea that NDVI-I provides a reasonable surrogate for ANPP at individual sites through time. We also assumed that the temporal relationship between NDVI-I and ANPP is consistent among vegetation types. The theoretical basis for estimating ANPP from the NDVI lies in the more fundamental link between the NDVI and the fraction of photosynthetically active radiation absorbed by plants (Sellers and others 1992). Monteith's (1972) formulations equate NPP to the product of photosynthetically active radiation absorbed over a specific period and an energy conversion efficiency coefficient, ϵ. Because ϵ may vary among species and seasonally within a single vegetation type (Pineiro and others 2006; Running and others 2004), the slope of temporal ANPP–NDVI-I relationships may not be constant through space and time. To what extent variation in ϵ might complicate interpretations of PMR is unclear. Also not clear is the extent to which soil color and vegetation structure might influence PMR, even though the NDVI's sensitivity to these two attributes is known to limit the index's usefulness for making spatial comparisons of ANPP and other vegetation characteristics (Holm and others 2003; Huete and Jackson 1987; Huete and others 1985).

Linear models were used to assess the strength of relationships between ANPP and NDVI-I at six long-term monitoring sites in our study area through time (Figure 5). ANPP emerged as the lone significant effect in all cases, indicating that between-site differences in vegetation and other characteristics did little to obfuscate the response of NDVI-I to inter-annual ANPP fluctuations. These results also confirmed that, at both annual and seasonal scales, the slope of ANPP–NDVI-I relationships did not differ significantly among the monitoring sites and vegetation types studied. In summary, the NDVI-I metrics considered here appear to strongly predict annual and summer-fall ANPP, and modestly predict spring ANPP, at individual Chihuahuan Desert sites through time. Although these results support the use of NDVI-I to study temporal ANPP dynamics in our region, sites dominated by honey mesquite were absent from our analyses, and we can not rule out the possibility that spatial patterns in PMR may also arise from factors not related to actual ANPP dynamics (for example, through differences in the optical properties of grass and shrub-dominated areas).

Mapping Plant Life Form Cover

Regardless of the mechanisms, the slope of the relationship between annual NDVI-I and 2-year cumulative precipitation was found to be an effective predictor of shrub canopy cover. NDVI-based PMR thus shows promise as an attribute for mapping ecological states in the region. One benefit of this approach is, presumably, the low sensitivity of temporal precipitation–NDVI-I relationships to spatial precipitation variability. We compared the performance of PMR to that of more straightforward measures of temporal NDVI variation such as range and coefficient of variation (CV). Our results indicate that the CV of late season NDVI-I from 2002 to 2009 was as good a predictor of shrub canopy cover ($r^2 = 0.71$) as was the slope of the relationship between annual NDVI-I and 2-year cumulative precipitation (Figure 3).

Thus, mapping efforts may not necessarily benefit from explicitly defining relationships between precipitation and NDVI-I. Indeed, most studies that have successfully used inter-annual NDVI response to map vegetation attributes of interest have not included precipitation measurements in their analyses. Rather, such investigations have focused on NDVI differences between high and low precipitation periods. For example, the heightened NDVI response of the exotic annual grass *Bromus tectorum* relative to that of native vegetation was successfully used to map *B. tectorum* occurrence across the US Great Basin (Bradley and Mustard 2005). Similarly, the range of NDVI values between years of contrasting rainfall proved useful for mapping areas with high cover of annual plants in the Mojave Desert (Wallace and Thomas 2008). For areas larger than the one studied here, explicit relationships between NDVI-I and precipitation might indeed generate superior results. Nevertheless, the comparable performance of a simple NDVI statistic in our study can be viewed as an encouraging outcome considering that dense rain gauge networks are absent across much of the globe and the spatial resolution of most satellite-based precipitation estimates is currently much coarser than that of MODIS imagery.

Conclusions

In managing the long-term value of a landscape, it is useful to distinguish ephemeral vegetation dynamics from transformations that might be impossible or impractical to reverse. Transformations belonging to the latter category are often instigated by changes in the dominant plant functional type, with subsequent effects on physical and biological processes. In this study, we have highlighted one aspect of ecological functioning potentially affected by landscape scale state change: the response of ANPP to inter-annual rainfall fluctuations. Using time-integrated NDVI as a measure of ANPP, we observed clear trends in PMR along a gradient of shrub encroachment in the northern Chihuahuan Desert. Differences between grass and shrub-dominated sites were largely consistent with physiological and morphological tradeoffs associated with woody and herbaceous plant life forms, although factors unrelated to ANPP cannot be discounted. In addition to sharpening the view of ecological dynamics in the region, these results illustrate the potential for using inter-annual NDVI variability to help map and monitor ecological states that are heterogeneously distributed at broad spatial scales, even when long-term average NDVI of these states is similar. Longer satellite time series and increased availability of high resolution precipitation estimates will promote the utility of this approach for detecting ecological state changes involving shifts in plant functional type dominance.

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