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Vegetation response to rainfall pulses in the Sonoran Desert as modelled through remotely sensed imageries

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ABSTRACT: In northwestern Mexico in an annual cycle comprised months 2008–2009, we estimated the effects of cumulative rainfall and previous vegetation status on current vegetative greenness adjusted for soil reflectance [via the Transformed Soil Adjusted Vegetation Index (TSAVI)] and canopy water content [via the Normalized Difference Infrared Index (NDII)]. Sample kernels (540 of <0.4 ha) were stratified in nine areas by latitude, distance to the Pacific Ocean and slope across a 15 000 km^2 area on the Baja California peninsula. Rainfall data were accumulated over 2-, 4- and 6-week periods from daily satellite estimates [via the Tropical Rainfall Measuring Mission (TRMM)]. TSAVI and NDII were calculated from Landsat 5 TM images. When restricted by season, multiple regressions results were $0.59 < r^2_{adj} < 0.96$ for TSAVI and $0.45 < r^2{}_{adj} < 0.85$ for NDII. Rainfall alone accounted for up to an exceptional 70% of the variance in vegetation indices, while the most widely significant factors were the previous vegetation status and its interaction with precipitation. For TSAVI, direct dependence on precipitation was generally much greater for the 4- and 6-week accumulation than for the 2-week periods. However, none of the factors was universally significant for either vegetation index. Results also showed the importance of scale in the spatial heterogeneity of climate and topography in this arid landscape.

KEY WORDS phenology; precipitation effects; TSAVI; NDII; TRMM; geographic template; slope effects

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1. Introduction

Net primary production increases across biomes within a range of increasing mean annual precipitation (Webb *et al.*, 1978; Le Houérou *et al.*, 1988), as does the stature of woody vegetation (Veillon, 1963). This observation may be valid in arid ecosystems, at least where dominated by herbaceous plants (Seely and Louw, 1980; Muldavin *et al.*, 2008), although by further analysis, productivity may depend more on the size and frequency of rainfall events or subseasonal accumulation (Nicholson *et al.*, 1990) than on the annual total (Reynolds *et al.*, 2004; Thomey *et al.*, 2011). Growth may occur after multiple rainfall events, and the timing and efficiency of growth varies among growth forms or functional types (Paruelo and Lauenroth, 1998; Reynolds *et al.*, 2004; Fabricante *et al.*, 2009; Nano and Pavey, 2013). This variation intensifies response patterns and complicates regional and inter-regional synthesis and comparison.

There is an inherent problem in the current responses of perennial plants; they are not independent of previous response patterns. This phenomenon depends mainly on the longevity of individual leaves and is more obvious at shorter intervals. However it is also apparent at seasonal and inter-annual intervals, and is definitely part of the dryland paradigm of pulse-reserve (Ogle and Reynolds, 2004; Thomey *et al.*, 2011). Therefore, it is essential to have accurate knowledge of the previous vegetative condition. Moreover, there are other variables that require consideration. These include substrate, topography, and geographic position, which clearly manifest heterogeneity at broad scales (Herrmann *et al.*, 2005a) and show patterns correlated with vegetation studied in smaller scale formats (Franklin, 1995; Deng *et al.*, 2007). Simultaneous sampling across a range of scales in time and space is an important challenge in the study of extremely water-limited ecosystems.

Characterization of vegetative landscapes can be facilitated by remote sensing, contributing to the study of factors that vary over much larger areas than are usually treated in plot-based field studies and that may not have constant effects at broader geographic scales (Herrmann *et al.*, 2005a; Fabricante *et al.*, 2009; Miller and Hanham, 2011). The vast majority of vegetation studies use the Normalized Difference Vegetation Index (NDVI), but when considering the modest degree of ground cover in arid regions, greenness may be better represented by the Transformed Soil Adjusted Vegetation Index (TSAVI; Baret and Guyot, 1991). Additionally,

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given the fact that plant moisture is clearly an important property in water-limited systems, the Normalized Difference Infrared Index (NDII; Hardinsky *et al.*, 1983) is an interesting alternative to other greenness indices (Deng *et al.*, 2007). The NDII is not responsive to chlorophyll content, variations of leaf internal structure, or leaf dry matter content, but it accurately quantifies the vegetation water content (Cheng *et al.*, 2008). In an arid shrubland, the NDII and greenness indices responded to exceptional rainfall, but only NDII showed a strong seasonal pattern, perhaps reflecting of trends in succulence (Rodríguez-Moreno and Bullock, 2013). In some circumstances, however, the NDII may also be affected by moisture on the ground surface (Hunt and Yilmaz, 2007).

Our purpose in this work was to examine that in an arid environment the responses of vegetative greenness and wetness to 'pulses' of rainfall, studied as the rainfall accumulated over periods ranging from two to several weeks. The vegetation was characterized by TSAVI and NDII for 60 m kernels from the widely used, fortnightly surface-reflectance data of Landsat 5 TM. For rainfall estimates, extensive data were derived from the satellite sensors of the Tropical Rainfall Measuring Mission (TRMM) which estimates daily rainfall for 27 km pixels (without internal structure). We also weighed these responses relative to previous condition of the same vegetation, to local topographic variation, and to larger variations in elevation and geographic context. Thus, we used small fixed plots, with substantial replication and distinction between kernels with low and steep slope gradients. We complemented local replication (within 25 km^2) with a stratified sampling (3×3) on latitude and longitude gradients. The study encompassed a challenging 15 000 km^2 region, with greater climatic and life-form diversity than generally typifies productivity studies using either remote sensing or ground methods. Owing to the intensity and magnitude of data analysis, a single year was examined. Despite the large amount of data and its analysis, the sources of random error were substantial, and so our interpretation qualifies the statistical comparisons, and combines limited assertion with suggestions for further work.

2. Materials and methods

2.1. Description of the study area

The region studied is in the Sonoran Desert, located in the central portion of the Baja California peninsula in northwestern Mexico. This section of the peninsula is <80 km wide with the east coast bordering the warm waters of the Gulf of California and the west coast bordering the cool California current along with cooler upwellings. A substantial and relatively reliable part of the precipitation regime occurs in winter, with southerly tracks of large frontal systems from the northeast Pacific (Minnich *et al.*, 2000); jet streams from the subtropical Pacific sometimes connect to and augment the northern storms (Dettinger, 2004). There is also summer precipitation during the Mexican monsoon (Douglas *et al.*, 1993), from events of varied meteorology, scale, and intensity. Precipitation is exceedingly variable in both regimes (Bullock, 2003). Summer events are more often localized, but it also occurs in some large and intense events. Previous analyses of precipitation have emphasized not only the latitudinal gradients but also a longitudinal configuration (García and Mosiño, 1968; Reyes Coca and Rojo Salazar, 1985) due to storm tracks, the contrast in Pacific and Gulf sea surface temperatures, and the intervening sierras of the peninsula.

Vegetation in the region includes a diversity of life forms, including deciduous shrubs, succulent rosette plants, cacti in a range of forms, softwood or succulent wood trees, evergreen sclerophylls, ephemeral therophytes, and other plant classes (Shreve, 1964; Humphrey, 1974; Turner and Brown, 1982), but their environmental sorting is not well understood. There is no grassland vegetation. The study region is largely within Mexico's federal natural protected area 'Valle de los Cirios'.

2.2. Sampling

Nine square sample areas ('polygons') of 25 km^2 were distributed within the study area (Figure 1), which corresponds to the peninsular land in the frame of Landsat 5 TM path 37 row 40. The important cross-peninsular dimension was represented by polygons at low to modest elevation near the Pacific coast, at interior or Cordillera locations, and at low elevation sites near the Gulf coast. A latitudinal dimension was represented by locating polygons in the northern, central and southern portions of the region. Polygon selection was constrained by several other criteria. Included among these criteria were the following: locations had to be close to the centroids of the pixels for precipitation measurement; areas were required to have multiple geomorphic units that would include categories of flat and steep sites – thus, an area with only one or two large alluvial fans or mountain scarps would be rejected; mesas were avoided as they are notoriously distinct from downslope flat areas, so the former were avoided. From a positive perspective, polygons were chosen which included at least two rock types, and in addition, our choice included polygons within which we selected sample points, rather than more dispersed points. This sample-point selection was done to delineate local areas for calculating soil lines and to simplify contrasts rather than assume gradient variation within the region.

We used slope gradient as another major variable because it affects vegetation development in many ways, through soil stability and development, hydrology, and exposure to solar radiation. Only two classes of slope were categorized: 'flat' sites were distinguished as having a slope between 0 and 10%, whereas 'steep' sites were defined as having a gradient greater than 35%. Within each polygon, these categories were mapped based on a digital elevation model with a 30 m grid. In each polygon, 30 sample points were chosen at random for each slope category. Two restrictions were applicable for

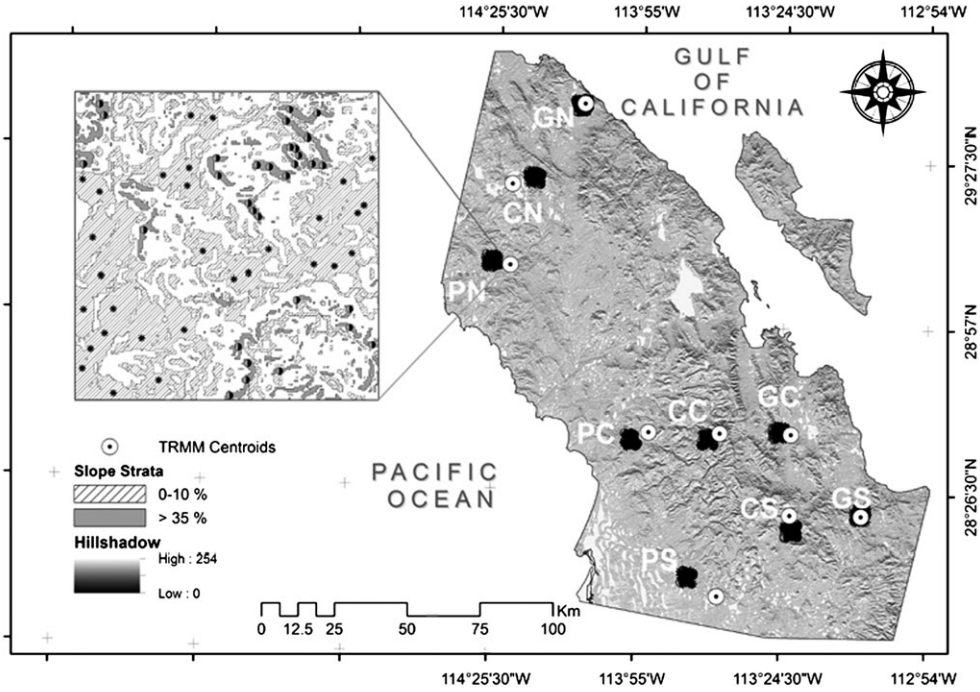

Figure 1. Distribution of sample polygons (names abbreviated) and an example with slope categories identified and sample points selected. The center of the TRMM pixel closest to each polygon is shown.

these selections: (1) the point had to be at least 60 m away from a first order drainage channel, and (2) the point had to be at least 100 m from its nearest neighbour. Each of these sample points was used to select the four closest adjoining pixels in Landsat 5 TM images. These pixel clusters constituted kernels for this study.

Daily precipitation data were derived from satellite observations of the Tropical Rainfall Measuring Mission (TRMM) for 0.25° grid cells (ground spacing of c. ~27.5 km). Details of the TRMM theory, sensors, imaging, and products have been provided by Huffman *et al.* (2007) and others. Owing to the periodic schedule of Landsat imagery and hence the vegetation indices, the daily rainfall data were accumulated over many days. Three periods in the summation of rain data were considered: 2, 4 and 6 weeks before each Landsat image date.

Temporal vegetation variability was captured with 15 Landsat 5 TM images; substantially cloud-free image dates were selected. These dates were: in 2008 – June 20, July 6, August 7, September 8, October 10, October 26, November 11, December 29; in 2009 – January 14, January 30, March 3, March 19, April 4, April 20, and May 6. Several dates in the schedule of Landsat 5 TM had extensive cloud cover, and unfortunately these were in the winter growing season, which affected our selection of the intra-seasonal interval for pulse-response analysis. (Some other satellite products are composited over many days to present only clear-sky conditions.) The data were subjected to relative radiometric, atmospheric, and topographic (illumination) corrections (Rodríguez-Moreno and Bullock, 2013) and were averaged among the four pixels of each kernel.

Two vegetation indices were calculated for each kernel date, representing greenness adjusted for incomplete canopy cover along with soil reflectance (TSAVI, Equation 1, Baret and Guyot, 1991) and canopy moisture (NDII, Equation 2, Hardinsky *et al.*, 1983).

$$\mathrm{TSAVI} = \frac{\beta_1\,(\mathrm{NIR} - \beta_1 \mathrm{R} - \beta_0)}{\beta_0 \mathrm{NIR} + \mathrm{R} - \beta_1 \beta_0 + 0.08\left(1 + \beta_1^2\right)} \quad (1)$$

$$\mathrm{NDII} = \frac{(\mathrm{NIR\text{-}SWIR})}{(\mathrm{NIR} + \mathrm{SWIR})} \quad (2)$$

In Equations 1 and 2, R stands for the red band (0.63–0.69 µm), NIR for the near infrared band (0.76–0.90 µm), and SWIR for the shortwave infrared band (1.55–1.75 µm). In Equation 1, β_1 is the slope of the soil line (the relation of R to NIR) and β_0 is the intercept (Fox *et al.*, 2004). TSAVI equals 0 for bare soils and is close to 0.70 for very dense canopies (Baret and Guyot, 1991). The range of NDII is −1 to +1. The parameters for TSAVI were determined for each date, polygon and slope category (with 120 pixels).

For the statistical analysis, we used normal descriptive statistics and skewness, *t*-test of group means, and multivariate linear regression as well as the Mann–Whitney test and the Kruskal–Wallis tests with multiple comparisons. There were six independent variables in all regressions: the accumulated rainfall of the preceding 2-, 4-, and 6-week periods; the vegetation index from the preceding image, and that index multiplied by the accumulated rainfall of the previous 2- and 4-week periods. Rainfall data were uniform in a polygon for a given date, whereas current and previous vegetation indices were specific to each kernel. Thus, sample sizes for the regressions were: 450 in each polygon and slope category for the year-long analysis; 120 for August to October; and 150 for March to May, with some losses due to aberrant data.

3. Results

3.1. Precipitation

In this year of study rainfall was heaviest in late summer. The single most notable event was tropical storm Julio, which came close to the southeast corner of our study area on 26 August 2008. This signal was barely present in the Pacific polygons, but was very prominent in the Gulf South polygons (Figure 2). Other significant summer events occurred which affected all Cordillera and Gulf polygons. Winter rainfall in this year of study was very sparse in the Pacific polygons and more substantial in the northern Cordillera and Gulf areas, particularly late in the season. Another notable feature for the region was that almost all rain events were <5 mm for all polygons, except for the summer season (Figure 2).

The Cordillera North polygon had the largest number of days with rain (79) and the Pacific South polygon had the least (14). Total rainfall for the year was greatest in the Cordillera polygons. Considering all the polygons together, the correlation between the number of days with any rain and total rain for the year was 0.79 ($p = 0.012$), suggesting that important extreme events did not overwhelm a substantially normal and incremental precipitation regime.

The maximum 6-week accumulation varied by 12.5 times between extremes in the Pacific Central and Gulf South polygons. An important feature to emphasize is that only two polygons showed maximums for 6 or 4 weeks that were substantially greater than the 2-week maximum. This highlights the infrequency of rain events in this region of the Sonoran Desert.

3.2. Variation in vegetation indices with slope and location

For TSAVI, there was heterogeneity for flat sites, which emphatically suggests providing separate analyses subsequently for each polygon separately (Figure 3). There was less heterogeneity among steep sites, although the northwest and southeast polygons differed from most others. For NDII, there were no significant differences among polygons within slope categories.

The ranges of TSAVI and NDII values are presented in Figure 3, along with the results obtained by comparing steep and flat sites within each polygon. Owing to the notable skewness in many cases and the contrasts in skewness between flat and steep strata, these categories were compared using the nonparametric Mann–Whitney test. Analysing the annual maximum results in TSAVI data, all except one of the polygons (Gulf Slope) showed significant differences between slope categories, but not always in the same sense; steep kernels generally had higher maximum TSAVI results. Minimum values of TSAVI also differed between flat and steep strata, except in the Gulf North polygon, and in all cases the less negative TSAVI values were in flat kernels.

The analysis of NDII data showed fewer and more biased differences between slopes categories: only three of the polygons showed differences in the annual maximum values of NDII data (Figure 3), but for minimum NDII values, only one polygon failed to differ between slopes categories. Thus, as measured using the NDII index, the vegetation canopy water content had less variation between slope categories than shown by TSAVI data.

3.3. Local greenness and wetness in relation to precipitation

The multi-temporal analysis of the vegetation indices, relative to prior rainfall and prior vegetation condition, was performed separately for each polygon and slope class. Given the spatial and temporal heterogeneity in precipitation (Figure 2), we also analysed three time periods: one encompassing the entire year, another comprising the late monsoonal period from August to October, and the third embracing the spring months of March–May. Thus there were two slope categories, nine polygons, three time periods, and two vegetation indices, resulting in 108 multiple regressions.

3.3.1. Transformed Soil Adjusted Vegetation Index

In the entire year's analysis, regressions were significant for flat sites $0.49 \le r^2_{\mathrm{adj}} \le 0.78$ except in the Pacific North and Gulf North polygons (Table 1). None of the accumulated precipitation variables alone contributed as much as 0.20 on flat sites except for the Gulf South polygon, although the three periods combined were influential in the Cordillera North (total of 0.47). The regressions for steep sites were somewhat weaker ($0.27 \le r^2_{\mathrm{adj}} \le 0.55$). In contrast to the flat sites, a contribution of at least 0.20 to r^2_{adj} was made by some precipitation variable alone, except in the North and the Pacific regions, but the relevant period varied from 2 to 6 weeks (Table 1). The most widely significant factor (17 of 18 cases) was TSAVI of the previous observation date, although it showed a large range of contribution ($0.02 \le r^2_{\mathrm{adj}} \le 0.49$). It is therefore apparent that vegetation was not generally static, although the timing and causes of changes in the regions were not uniform, or obvious.

For the August to October period, seven polygons showed strong regressions on flat sites ($0.87 \le r^2_{\mathrm{adj}} \le 0.95$). The Cordillera Central and Pacific South polygons were the exception (Table 2). The 6-week accumulated precipitation was most important in the North, whereas the 4- or 6-week periods were pre-eminent in the South (with $r^2_{\mathrm{adj}} < 0.75$). The Central and South tiers were more varied and showed the greater importance of the previous state of the vegetation. For steep sites, the regressions were only slightly weaker, with $0.63 \le r^2_{\mathrm{adj}} \le 0.93$ with the exception of the Cordillera Central polygon. In the South, 4- and

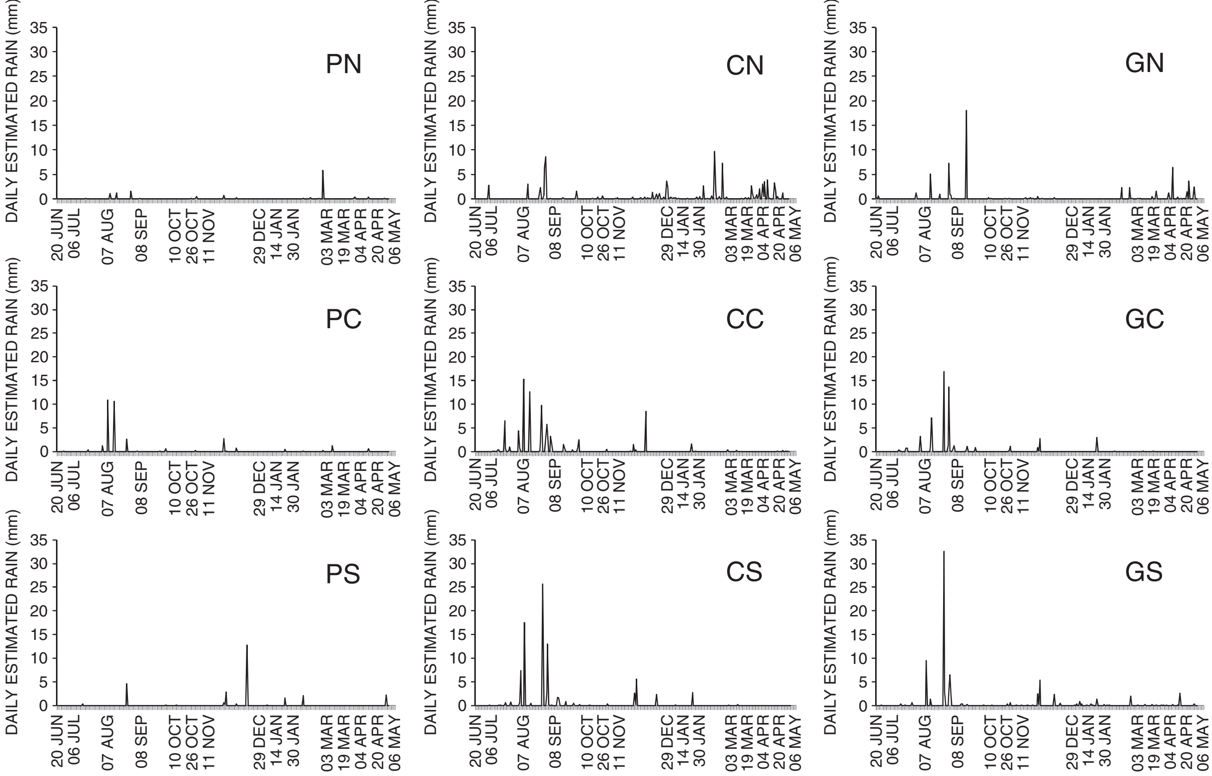

Figure 2. Daily rainfall estimated by TRMM, from 9 May 2008 to 6 May 2009, for each polygon. From left to right: Pacific, Cordillera and Gulf; from the top to down: North, Central and South. Date labels are shown for Landsat image dates.

6-week precipitation sums were most important. The relative importance of each factor, however, was not similar between flat and steep sites within polygons. This period of subregionally heavier rain in the study year had variation more fully comprehended by the models, although notable variations affecting the models were introduced by local conditions, including substrate, exposure to the storms and perhaps also related to vegetation composition.

For the March–May period, the regressions for flat sites were somewhat weaker than for the August–October period, with $0.60 \leq r^2_{adj} \leq 0.83$ except for relative weakness in the Pacific South and Gulf South polygons (Table 2). Precipitation was the strongest factor in the North and Central tiers, especially the 6-week accumulation, exceeding somewhat the summer slowdown. The steep sites experienced a still lower impact, with a value of $0.26 \leq r^2_{adj} \leq 0.68$. No factor maintained its importance among polygons in north–south or east–west directions for steep sites in this period, reflecting perhaps limited moisture infiltration with the less-intense rains.

3.3.2. *Normalized Difference Infrared Index*

Regressions for the entire year showed a wide range of power in NDII data among the polygons ($0.01 \leq r^2_{adj} \leq 0.87$), with less difference between flat and steep sites than in TSAVI values (Table 1). The lowest values occurred in the Pacific North and the highest in the Gulf Central polygons; the Gulf polygons registered the strongest correlations. The determining factors were generally the interaction of the vegetation's previous state with a small influence of rainfall. Precipitation most clearly affected NDII values in the Central tier, to a greater extent for both flat and steep sites in the Gulf Central polygon during the short, 2-week accumulation period, and notably at 4 weeks for flat strata and 6 weeks for steep sites in the Cordillera Central and Pacific Central polygons. This heterogeneity in the timing of water distribution suggests that plant water availability is influenced by two factors: the soil permeability along with its capacity for water retention, and that the polygons differed with respect to the dominance of different plant types.

For the August–October period, the level of determination was generally high ($0.51 \leq r^2_{adj} \leq 0.90$) with the striking exception of the Cordillera Central polygon ($r^2_{adj} < 0.23$), and varied minimally between flat and steep sites (Table 2). The predominant factor for both slope classes in all Pacific polygons was NDII_{t-1}, and this was the same for slope classes within the Cordillera polygons, although differing from north to south. Factors in the Gulf polygons were not as consistent, but several strong effects of precipitation in the preceding 2 weeks contrasted with the Cordillera and Pacific polygons.

In the March–May period, flat and steep sites registered quite similar in level of determination ($0.46 \leq r^2_{adj} \leq 0.84$, except lower in the Pacific Central) with the highest values evident in the Gulf Central

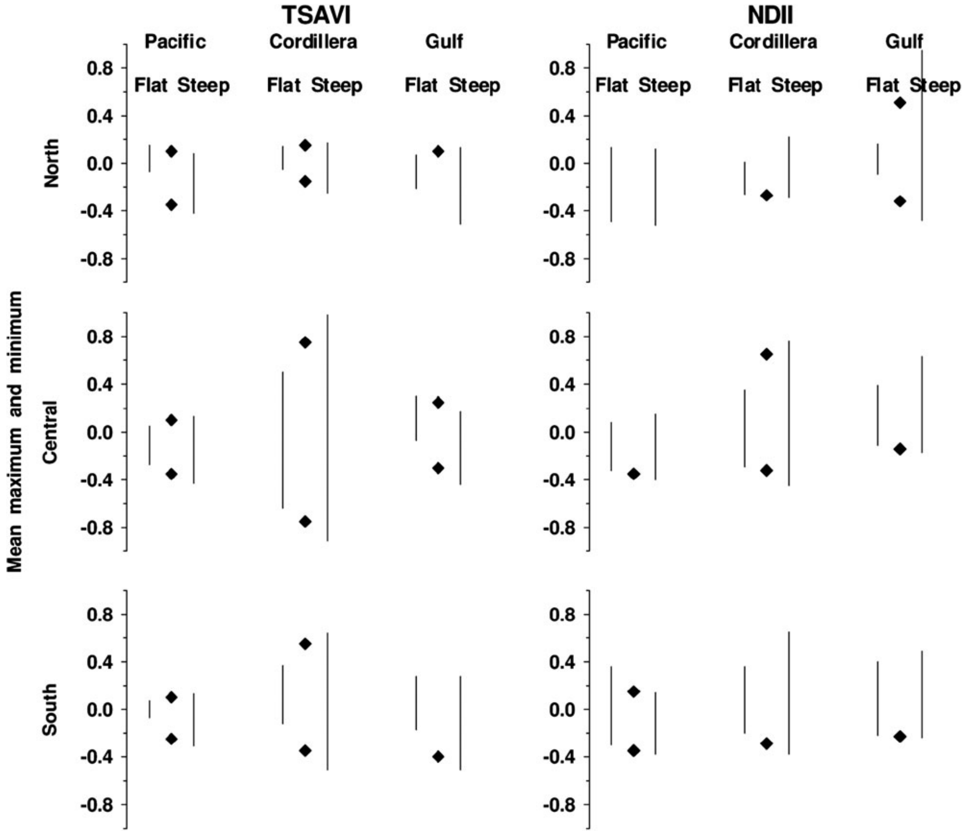

Figure 3. Range of variation of each vegetation index in the entire year (means of maximum and of minimums among the 30 kernels) for each polygon and slope class, with indication (diamonds) of significant differences between slope classes.

polygon (Table 2). The predominant factor in the north was precipitation over 6 weeks in Pacific and Cordillera polygons, but over only 2 weeks for Gulf polygons. The value of $NDII_{t-1}$ predominated for the Gulf Central polygon while it shared importance with precipitation for both Pacific and Cordillera Central polygons. There was a strong tendency for major effects on NDII to be more similar locally, between flat and steep categories, than among polygons. In this regard, moisture retention due to soil microbes may merit attention (Rodríguez-Moreno and Bullock, 2013).

4. Discussion

The concept of arid ecosystems as rainfall-pulsed systems has been modified in recent years. Responses are limited to above-threshold conditions of soil moisture, which depend on cumulative inputs and losses as well as on the condition of the plants, which can be affected by events in previous months or years (Herrmann *et al.*, 2005b; Fabricante *et al.*, 2009) and also on species adaptations (Reynolds *et al.*, 2004; Shen *et al.*, 2005). Similarly, our results showed that increases of greenness and water content in the vegetation canopy varied depending upon accumulated development of the plants and on more or less recent rainfall, but in a variety of combinations and to a highly variable degree. Those variations were distributed between slope categories at a local level, and among sites in this regionally mountainous landscape. Seasonal variations were also important, with models for both late summer and spring being stronger than the annual models, but in any one polygon, the seasonal models were not close to each other in structure. Soil types and hydrology clearly merit more attention but they are difficult to comprehend regionally, with high resolution in this inaccessible area. Considering this limitation, the lack of ground vegetation samples, the low resolution of precipitation estimates, and the limitation to conditions of 1 year, the models were remarkably good. Notably, our results showed that a linear approximation of pulse and response was generally a useful first approximation.

The local, regional, and temporal heterogeneity of model structure and strength raise further questions about the ways these responses may be affected by the composition of the vegetation regarding growth forms or functional types. There appears to be ample possibility of diversity in types among the perennials, considering structural types and phenology (Shreve, 1964; Kemp, 1983; Turner *et al.*, 1995), as well as leaf properties (Rodríguez-Moreno, 2012). While seasonal limitations of vegetative activity are scarcely known in the study region, multiple modes of response are probably present among the diverse ‘shrub’ flora (Franco-Vizcaíno, 1994). Clearly, one element of difference among forms is the formation and disposition of reserves as discussed in the

Table 1. Multiple regression of present vegetation state (TSAVI or NDII) on previous vegetation state and precipitation accumulated over 2, 4 or 6 weeks (2R, 4R or 6R), during the entire year of June 2008–May 2009.

All year	Factor	TSAVI							NDII					
		Pacific		Cordillera		Gulf			Pacific		Cordillera		Gulf	
		Flat	Steep	Flat	Steep	Flat	Steep	Factor	Flat	Steep	Flat	Steep	Flat	Steep
North	Regression	**0.26**	**0.55**	**0.66**	**0.34**	**0.08**	**0.27**	Regression	**0.01**	**0.04**	**0.16**	**0.24**	**0.26**	**0.32**
	$TSAVI_{t-1}$		0.24	0.17	0.15	0.05	0.10	$NDII_{t-1}$		0.03		0.18	0.02	0.01
	$TSAVI_{t-1}$ *2R	0.03	0.02	0.01	0.15		0.09	$NDII_{t-1}$ *2R						0.01
	$TSAVI_{t-1}$ *4R	0.03	0.14	0.01	0.02			$NDII_{t-1}$ *4R			0.13		0.08	0.21
	2R	0.05	0.02	0.15		0.03	0.03	2R	0.02		0.02		0.15	0.09
	4R	0.09	0.12	0.14				4R				0.05		
	6R	0.05		0.18	0.03		0.05	6R					0.01	0.02
Central	Regression	**0.64**	**0.36**	**0.50**	**0.30**	**0.78**	**0.43**	Regression	**0.44**	**0.29**	**0.39**	**0.24**	**0.87**	**0.73**
	$TSAVI_{t-1}$	0.24	0.11	0.22	0.02	0.10	0.12	$NDII_{t-1}$	0.26	0.04	0.14	0.09	0.05	0.11
	$TSAVI_{t-1}$ *2R	0.04	0.08	0.05		0.03	0.03	$NDII_{t-1}$ *2R	0.03	0.12				0.06
	$TSAVI_{t-1}$ *4R	0.16	0.02		0.03	0.61	0.02	$NDII_{t-1}$ *4R	0.03		0.06		0.31	
	2R	0.17		0.06		0.01		2R			0.03	0.04	0.49	0.52
	4R	0.01	0.14	0.13	0.21	0.03		4R	0.11		0.14	0.02	0.01	
	6R	0.03		0.06	0.05	0.01	0.25	6R		0.10		0.10	0.02	0.04
South	Regression	**0.49**	**0.43**	**0.66**	**0.40**	**0.60**	**0.34**	Regression	**0.36**	**0.47**	**0.33**	**0.21**	**0.23**	**0.13**
	$TSAVI_{t-1}$	0.49	0.22	0.21	0.17	0.07	0.03	$NDII_{t-1}$	0.02	0.35	0.20		0.22	0.07
	$TSAVI_{t-1}$ *2R		0.01	0.22	0.01	0.21		$NDII_{t-1}$ *2R	0.18		0.11	0.05		0.03
	$TSAVI_{t-1}$ *4R	0.01	0.01	0.02			0.06	$NDII_{t-1}$ *4R	0.06	0.02	0.02	0.04	0.01	
	2R			0.18	0.20	0.02		2R	0.01	0.02		0.09		0.02
	4R		0.19			0.01	0.22	4R	0.06	0.05		0.03		
	6R			0.03	0.02	0.29	0.03	6R	0.04	0.04				

All $p < 0.05$ with Bonferroni correction. The numbers tabulated are r^2_{adj} for the entire model (bold) and for the contribution of each factor. Non-significant factors are blank.

pulse-reserve models (Reynolds *et al.*, 2004). Another is the efficiency of resource use that affects the longevity of green and/or moist tissue. Our models suggest that this issue has broad relevance. It seems evident that the substrate itself deserves more attention than our preliminary treatment of geomorphology (Herrmann *et al.*, 2005a; Notaro *et al.*, 2010; Svoray and Karnieli, 2011). These elements are manifest in simpler but broadly variable steppes in Patagonia, studied with remote sensing and the NDVI (Fabricante *et al.*, 2009).

Most daily precipitation in dryland areas is relatively small (<5 mm). These small inputs have been shown to have ecological value (Sala and Lauenroth, 1982), if their amount and pattern in relation to evaporation allow soil moisture reserves to be created or augmented. This was apparent in some of our results where an increase in greenness was related to precipitation accumulated over a month or more of occasional days with only a few millimeters of precipitation. These rains occurred in the temperature and radiation conditions of winter and spring, which should have ameliorated evaporation. The exceptionally strong, short pulse of precipitation brought by tropical storm Julio at the end of August showed different levels of impact on greenness and wetness between slope categories and among polygons.

As with previous work in this region (Rodríguez-Moreno and Bullock, 2013), this study emphasizes that spatial variation in environment highlights the importance of each variable in the subregional models and suggests that their 'nonstationarity' of drivers (Miller and Hanham, 2011) merits more attention. This was true not only at the regional scale for climate, but also locally for slope, with the greater contrasts apparent between flat and steep sites registered by the TSAVI than the NDII. Local variation and soil hydrology are complex issues but require attention as shown here, as well as in non-mountainous terrain (Farrar *et al.*, 1994). The central cordillera in particular had the lowest continuity of conditions of both flat and steep terrain, undoubtedly affecting soil hydrology and perhaps also the heterogeneity of vegetation composition among sample kernels.

Regarding the NDII's utility, Cheng *et al.* (2008) showed that this index was related to vegetation water content and canopy cover in a variety of arid habitats. Our results do not suggest that NDII generally reflects soil moisture because of the weak or nil effect of short-term rainfall, with the remarkable exception of most Gulf polygons in both slope classes and in both seasons. The general lack of correspondence between TSAVI and NDII models is both a challenge and opportunity (Deng *et al.*, 2007). It appears evident, therefore, that greenness and canopy water content were not engendered together. Plants with succulent leaves and/or stems are diverse and common, as well as non-uniform in distribution (Humphrey, 1974; Turner and Brown, 1982), and their effect on NDII requires elaboration.

This work not only produces some surprisingly strong linear models, but also suggests further studies needed to improve the scaling of the models, verify some underlying data, and to provide insight into the effects of variable composition of the vegetation. Clearly, multi-year studies are required for exploring other rainfall

Table 2. Multiple regression of present vegetation state (TSAVI or NDII) on previous vegetation state and precipitation accumulated over 2, 4 or 6 weeks (2R, 4R or 6R). Data from August 2008 to October 2008 and from March 2009 to May 2009.

August to October	Factor	TSAVI							NDII					
		Pacific		Cordillera		Gulf			Pacific		Cordillera		Gulf	
		Flat	Steep	Flat	Steep	Flat	Steep	Factor	Flat	Steep	Flat	Steep	Flat	Steep
North	Regression	**0.94**	**0.86**	**0.94**	**0.89**	**0.87**	**0.63**	Regression	**0.90**	**0.79**	**0.76**	**0.51**	**0.86**	**0.61**
	$TSAVI_{t-1}$	0.18	0.14	0.41	0.40	0.21	0.09	$NDII_{t-1}$	0.78	0.57	0.62	0.52	0.02	
	$TSAVI_{t-1}$ *2R		0.04		0.25	0.18	0.10	$NDII_{t-1}$ *2R					0.02	0.06
	$TSAVI_{t-1}$ *4R	0.01	0.22		0.03		0.18	$NDII_{t-1}$ *4R		0.06	0.10		0.25	0.40
	2R	0.02			0.05	0.06	0.06	2R					0.52	0.16
	4R	0.04	0.33	0.04	0.03	0.14		4R	0.01				0.01	
	6R	0.69	0.14	0.49	0.14	0.29	0.15	6R	0.09	0.15			0.05	
Central	Regression	**0.95**	**0.93**	**0.44**	**0.31**	**0.93**	**0.89**	Regression	**0.87**	**0.74**	**0.23**	**0.19**	**0.65**	**0.83**
	$TSAVI_{t-1}$	0.36	0.27	0.06			0.53	$NDII_{t-1}$	0.70	0.48			0.01	0.02
	$TSAVI_{t-1}$ *2R	0.40	0.31				0.10	$NDII_{t-1}$ *2R						0.03
	$TSAVI_{t-1}$ *4R	0.18	0.06		0.03	0.92		$NDII_{t-1}$ *4R	0.02	0.14			0.37	0.12
	2R	0.02	0.27	0.02	0.28		0.05	2R		0.09				0.66
	4R	0.00	0.02	0.09				4R	0.15	0.03			0.54	
	6R			0.27		0.01	0.21	6R			0.21	0.17	0.02	
South	Regression	**0.41**	**0.88**	**0.95**	**0.65**	**0.92**	**0.88**	Regression	**0.88**	**0.88**	**0.75**	**0.80**	**0.86**	**0.75**
	$TSAVI_{t-1}$	0.41	0.06	0.14	0.10	0.06	0.15	$NDII_{t-1}$	0.75	0.54	0.03	0.06	0.26	0.35
	$TSAVI_{t-1}$ *2R		0.13				0.02	$NDII_{t-1}$ *2R	0.02		0.01		0.14	0.05
	$TSAVI_{t-1}$ *4R						0.16	$NDII_{t-1}$ *4R	0.01	0.16	0.23		0.03	0.07
	2R		0.23		0.14	0.09	0.03	2R	0.08				0.42	0.29
	4R			0.76		0.01	0.44	4R		0.04	0.49	0.75	0.02	
	6R		0.47	0.04	0.40	0.75	0.08	6R	0.01	0.14				

March to May		TSAVI							NDII					
		Pacific		Cordillera		Gulf			Pacific		Cordillera		Gulf	
North	Regression	**0.74**	**0.26**	**0.83**	**0.48**	**0.68**	**0.27**	Regression	**0.80**	**0.76**	**0.77**	**0.70**	**0.66**	**0.51**
	$TSAVI_{t-1}$	0.14		0.04	0.04	0.06		$NDII_{t-1}$			0.02	0.10		0.11
	$TSAVI_{t-1}$ *2R	0.01	0.21	0.02				$NDII_{t-1}$ *2R		0.04	0.02			
	$TSAVI_{t-1}$ *4R		0.06				0.04	$NDII_{t-1}$ *4R	0.02					0.12
	2R					0.15		2R					0.56	0.28
	4R	0.03		0.05	0.14	0.05	0.16	4R	0.30	0.20	0.09	0.15	0.02	
	6R	0.54		0.73	0.28	0.33	0.07	6R	0.49	0.52	0.63	0.43	0.07	
Central	Regression	**0.73**	**0.48**	**0.80**	**0.52**	**0.80**	**0.67**	Regression	**0.66**	**0.44**	**0.57**	**0.60**	**0.84**	**0.79**
	$TSAVI_{t-1}$	0.07	0.03	0.04		0.15	0.16	$NDII_{t-1}$	0.22		0.50		0.72	0.58
	$TSAVI_{t-1}$ *2R		0.07	0.10			0.14	$NDII_{t-1}$ *2R			0.02		0.09	0.10
	$TSAVI_{t-1}$ *4R	0.08		0.05	0.44	0.20		$NDII_{t-1}$ *4R				0.04		
	2R	0.32			0.08	0.09	0.32	2R	0.21	0.06				0.02
	4R	0.22		0.08				4R				0.19	0.02	0.05
	6R	0.05	0.37	0.54		0.37	0.07	6R	0.22	0.37		0.36	0.01	0.04
South	Regression	**0.30**	**0.68**	**0.60**	**0.58**	**0.26**	**0.28**	Regression	**0.46**	**0.5**	**0.71**	**0.65**	**0.62**	**0.68**
	$TSAVI_{t-1}$		0.04		0.39			$NDII_{t-1}$	0.03				0.01	0.05
	$TSAVI_{t-1}$ *2R		0.47	0.41	0.04	0.11		$NDII_{t-1}$ *2R		0.12	0.01	0.47	0.02	
	$TSAVI_{t-1}$ *4R	0.30	0.08	0.04		0.06		$NDII_{t-1}$ *4R	0.06	0.18	0.68		0.12	0.04
	2R		0.03	0.13	0.09		0.21	2R	0.08	0.03	0.01		0.37	0.52
	4R		0.02		0.05		0.04	4R	0.24	0.12		0.04	0.07	0.04
	6R		0.06			0.07		6R	0.07	0.07		0.15	0.04	0.03

All $p < 0.05$ with Bonferroni correction. The numbers tabulated are r^2_{adj} for the entire model (bold) and the contribution of each factor. Non-significant factors are blank.

patterns regarding both timing and amount, in addition to long-term effects. The 'natural experiments' covered here have been instructive but the potential variations are larger, especially for the cumulative effects of winter storms (Bullock, 2003). Also, the precipitation data derived from TRMM require verification by local ground stations. These data have been verified elsewhere and thereby support substantial confidence in their use (Huffman *et al.*, 2007; Dinku *et al.*, 2010; Javanmard *et al.*, 2010), particularly for multi-week summations. It remains plausible that peculiarities in meteorology might affect the calibration, especially for seasonal differences in this tropical–temperate transition region (Ebert *et al.*, 2007). A study of the remote and ground data may also provide an indication of how to interpolate the TRMM data to a much finer grid (Ji and Chen, 2012), thereby allowing a less rigid and limited spatial structure.

Satellite data for short-term, precipitation-driven variation in vegetation remain important for studies covering large areas or many plots and for inaccessible areas that hold particular interest pertaining to wildfires, range cattle (Baldassini, 2010), exceptional fauna (bighorn sheep and pronghorn antelope in the study region), and in general to other forms of exceptional biodiversity (Turner *et al.*, 2003). Moreover, Landsat provides good resolution for rough landscapes and well-defined times of measurement. Clouds, however, interfere with the formation of time series, and this demands both flexibility and innovation for addressing problems such as the response to rainfall events.

5. Conclusions

In this study, we explored the response of dryland vegetation to recent rainfall, using multi-temporal remotely sensed images for both components. No single model of response would serve across local topographic variation, or across even half the region, or through time. Variation in climate and plants was much more useful when analysed on a seasonal rather than annual basis. The recent state of the vegetation and rainfall accumulated over several weeks were dominant features of the regional ecosystem. Quick and strongly pulsed response required an extraordinary input. Models were generally different at a local level between flat and steep sites, and were probably further affected by local heterogeneity of topography and vegetation. The functional relation of greenness and wetness was not apparent, and much of the local and regional diversity of models may have been due to heterogeneous life form composition of the vegetation. Principal points for further study include the verification of satellite rainfall estimates, fine-scale hydrology, and the physiology of different plant life forms.

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