

# Functional differences between summer and winter season rain assessed with MODIS-derived phenology in a semi-arid region

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## Abstract

**Questions:** We asked several linked questions about phenology and precipitation relationships at local, landscape, and regional spatial scales within individual seasons, between seasons, and between year temporal scales. (1) How do winter and summer phenological patterns vary in response to total seasonal rainfall? (2) How are phenological rates affected by the previous season rainfall? (3) How does phenological variability differ at landscape and regional spatial scales and at season and inter-annual temporal scales?

**Location:** Southern Arizona, USA.

**Methods:** We compared satellite-derived phenological variation between 38 distinct 625-km<sup>2</sup> landscapes distributed in the northern Sonoran Desert region from 2000 to 2007. Regression analyses were used to identify relationships between landscape phenology dynamics in response to precipitation variability across multiple spatial and temporal scales.

**Results:** While both summer and winter seasons show increases of peak greenness and peak growth with more precipitation, the timing of peak growth was advanced with more precipitation in winter, while the timing of peak greenness was advanced with more precipitation in summer. Surprisingly, summer maximum growth was negatively affected by winter precipitation. The spatial variations between summer and winter phenology were similar in magnitude and response. Larger-scale spatial and temporal variation showed strong differences in precipitation patterns; however the magnitudes of phenological spatial variability in these two seasons were similar.

**Conclusions:** Vegetation patterns were clearly coupled to precipitation variability, with distinct

responses at alternative spatial and temporal scales. Disaggregating vegetation into phenological variation, spanning value, timing, and integrated components revealed substantial complexity in precipitation-phenological relationships.

**Keywords:** Bimodal; Modis; Phenology; Precipitation; Spatial variation.

## Introduction

Phenological dynamics of vegetation, including event timing, event value, and integrated time between events, exhibit substantial complexity in both space and time (Reed et al. 1994; White et al. 1997; Zhang et al. 2005). This variation directly affects individual plants (Chuine & Beaubien 2001), vegetation communities (Penuelas et al. 2004; Cleland et al. 2007), and ecosystem functioning (Foley et al. 2000; Picard et al. 2005), and is implicated as a critical biological response to global changes (Menzel et al. 2006; Cleland et al. 2007). Variation in vegetation phenology further affects diverse biophysical processes, with consequences for the linkages between ecologic, hydrologic, and atmospheric dynamics. A better understanding of the spatio-temporal variation in phenology will help to evaluate hypotheses on vegetation dynamics and constrain uncertainty in ecosystem functioning (Poveda & Salazar 2004). A growing theory of ecohydrological dynamics suggests vegetation organizes to maximize water usage (Eagleson 1982; Scanlon et al. 2005). Problems exist with this optimization theory (Kerckhoff et al. 2004), particularly when addressing the multiple-scale, dynamic vegetation response to changing water availability. Including phenological dynamics may help to improve understanding of vegetation-hydrologic linkages (Jenerette & Lal 2005). However, the sensitivity of phenology to water availability is, at present, not well understood. For example, two field experiments examining interactions between precipitation and phenology found strong overall responses; however, individual aspects of phenology responded distinctly (Penuelas et al. 2004; Cleland et al. 2006).

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Remote observation-derived phenology variables are becoming widely used to identify broad patterns in vegetation phenology and their relationships to environmental determinants. Remote observations of phenological patterns rely primarily on the use of regularly repeating, satellite-derived vegetation indices, often associated with leaf area, or more commonly with the absorbed fraction of photosynthetically active radiation (FAPAR) (Friedl et al. 1995). Common indices of greenness include the normalized difference vegetation index (NDVI) and, more recently, the enhanced vegetation index (EVI). EVI was developed specifically for applications using the newer Moderate Resolution Imaging Spectroradiometer (MODIS) sensors, with resulting reduced sensitivity to soil and atmospheric effects and higher sensitivity to green vegetation density, compared to NDVI (Huete et al. 2002). Early applications of satellite data for describing phenological dynamics began with the Advanced Very High Resolution Radiometer (AVHRR) (Reed et al. 1994; Myneni et al. 1996; Schmidt & Karnieli 2000) and continued with MODIS sensors (Zhang et al. 2005), providing a record of over 20 years (Barbosa et al. 2006). Repeat satellite imagery has shown strong correspondence with ground-measured phenological patterns across a broad range of biomes (White et al. 1997; Fisher & Mustard 2007; Maignan et al. 2008). Satellite-derived vegetation indices are often responsive to dynamics of water availability (Jolly & Running 2004; Park et al. 2004; Zhang et al. 2005). Data derived from remote observations allow investigation of broad-scale questions about phenological variation, complementing individual experimental manipulations (Liang & Schwartz 2009).

Regions with bimodal precipitation regimes provide unique conditions for improving understanding of how precipitation affects phenological variation. In bimodal precipitation systems, the interactions between precipitation and other climate variables, for example temperature, can be directly assessed in the same geographic location. Much of our understanding of the interactions between phenology and water availability is derived from studies

where precipitation arrives primarily in a single season (Maignan et al. 2008), even though multiple growing seasons within a year are often observed globally (Zhang et al. 2005). A resulting large uncertainty exists in understanding how multiple seasons of precipitation interact with vegetation (Fang et al. 2005). The North American Sonoran Desert is strongly limited by water, and precipitation is bimodal, generated by widespread and long-duration frontal systems in winter (Hastings & Turner 1965) and more localized and high-intensity convective storms in summer (Carleton 1987), leading to complex ecohydrological relationships in space and time (Drezner 2003). Along with the obvious temperature and light availability differences between seasons, several additional differences in rainfall are associated with seasonality. In comparison to winter rains, summer rains generally exhibit larger spatial variability, more frequent events, greater event intensity, more surface run-off, and higher evaporative demand (Goodrich et al. 2008). These summer-winter contrasts are common features of summer and winter rains globally.

The importance of precipitation for vegetation and the differences between summer and winter rains allow the examination of several coupled ecologic-hydrologic hypotheses (Table 1). At local spatial and single-season temporal scales, a principal hypothesis is that phenological variation scales with inter-annual precipitation variation due to a consistent water-use efficiency (WUE). A competing hypothesis suggests that, while precipitation is critical for ecosystem functioning, it acts as a driver for non-linear state changes between dormancy and active growth, and sensitivity to total seasonal precipitation may be reduced (Huxman et al. 2004b; Baldocchi et al. 2006; Potts et al. 2006). This hypothesis is consistent with studies showing that once water is available, alternate limits to productivity, for example nitrogen availability, are quickly reached (Padgett & Allen 1999; Harpole et al. 2007).

The above hypotheses do not discriminate between seasons; however, the contrasts in winter and summer precipitation characteristics may generate

**Table 1.** Hypotheses describing the effect of precipitation on phenological dynamics.

Processes	Hypotheses	Predictions
Effect of increased water on phenology	Consistent WUE	Linear response
	Switches	Independence above minimal threshold
Effect of prior season precipitation on phenology	Moisture priming	Larger/more rapid response
	Inhibitory	Smaller/slower response
Seasonal differences	Temperature-dependent metabolism	Summer larger/more rapid than winter
	Effective precipitation	Winter larger/more rapid than summer

several differences in vegetation responses to total precipitation. A temperature-dependent metabolic hypothesis (Brown et al. 2004) suggests that higher metabolic activity in summer will lead to larger and faster phenological responses than in winter. Alternatively, an effective rainfall hypothesis suggests that gains associated with higher temperatures may be countered by the decreased effective soil wetting for a given amount of precipitation due to losses from run-off and rapid evapotranspiration.

Complementing seasonal differences in phenological precipitation sensitivity, there may also be interactive effects between growing season rainfall and antecedent rainfall (Cable 1975). At the inter-seasonal scale, three competing hypotheses predict contrasting antecedent rainfall effects on within-season vegetation-precipitation relationships. A moisture-priming hypothesis suggests precipitation in the prior season primes vegetation for growth in the following season (Scott et al. 2008). Alternatively, summer and winter vegetation communities could be functionally distinct and insensitive to previous season rainfall. Finally, an inhibitory effect of prior rain has also been suggested – increased antecedent rains may lead to reduced vegetation sensitivity to within-growing season rainfall (Wang et al. 2001).

In addition to generating predictions of mean phenological responses, these hypotheses also lead to predictions for phenological spatial variability. At spatial scales broader than the individual local patch, the precipitation-dependent phenology hypothesis predicts strong correspondence between precipitation and phenology; however species differences and soil variation may also affect phenological patterns. Spatial variation in vegetation may either mute or amplify effects of spatial variation in precipitation. Similarly, soil characteristics, in particular texture, directly affect soil moisture status and allow for variation in effective moisture for the same amount of precipitation. The temperature-dependent metabolic hypothesis, the effective rainfall hypothesis, and convective storm characteristics suggest phenological patterns in summer will be much more variable than in winter.

Together, this suite of competing ecophysiological hypotheses describe multiple predictions for the effects of within-season precipitation, between-season precipitation, and inter-annual variation in precipitation on phenological variation.

Our objective was to evaluate the hypothesized functional relationships between precipitation and phenology across a range of spatial and temporal scales, and independently for the summer and winter

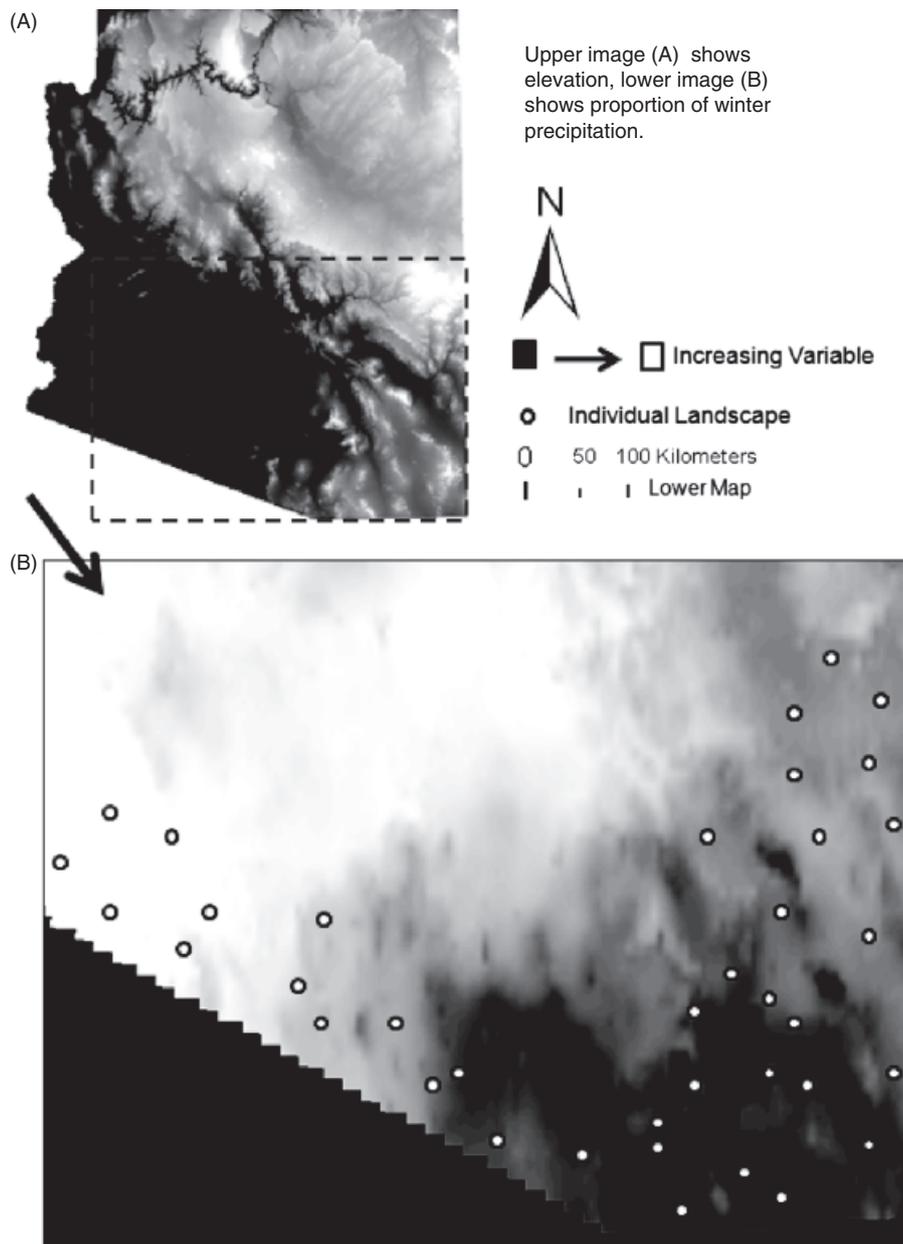
rainy seasons in the northern Sonoran Desert using remotely observed phenological patterns. In conducting this research, we asked several linked questions at local, landscape, and regional spatial scales and within individual seasons, between seasons, and inter-annually. (1) How do winter and summer phenological patterns vary in response to total seasonal rainfall? (2) How are phenological patterns affected by the previous season rainfall? (3) How does phenological variability differ at landscape and regional spatial scales and seasonal and inter-annual temporal scales? In asking these questions, we examined relationships at three temporal and two spatial scales to evaluate the multiple competing hypotheses describing precipitation-phenology relationships in water-limited systems. The multiple scale approach of our study, which uses scale differences to help discriminate between hypotheses, will help with future projections of vegetation responses to global change from a combined ecophysiological and landscape ecological approach (Wu & Hobbs 2002; Turner 2005).

## Methods

### *Data preparation*

We acquired 16-day repeat MODIS EVI imagery at 250-m resolution for 2000-2007 (from the Distributed Active Archive Center website, <http://edcdaac.usgs.gov/main.asp>), spatial patterns of monthly precipitation during the same time period, and additional GIS coverage including land cover and elevation for the southern Arizona region. The MODIS sensors obtain daily images and these data are composited into a 16-day repeating product that reduces the potential effects of clouds or other atmospheric scatter by reporting the single largest observed value for each pixel. As part of an initial data screening, we excluded cloud-contaminated pixels and interpolated the point from the nearest available four neighbors (Zhao et al. 2005). Monthly estimates of precipitation and temperature from 1900 to the present at a spatial grid size of 4 km were obtained from the PRISM database (PRISM Group, Oregon State University, <http://www.prismclimate.org>). These data have been extensively validated by comparison against 1800 weather stations, and reported values are within 1% of observed precipitation (Daly et al. 2002, 2008; Di Luzio et al. 2008).

Following data preprocessing using ArcGIS, the remaining analyses were conducted using



**Fig. 1.** (a) Surface elevation map of Arizona, ranging from 21 to 3850 m. (b) Study area in southern Arizona with locations of individual landscapes and precipitation during the winter months as a proportion of the total precipitation, ranging from 35% to 84% (background).

algorithms written in Matlab. From each scene, we extracted 38 individual landscapes of 625 km<sup>2</sup> (100×100 pixels) from the southern AZ region (Fig. 1). The landscapes were chosen using an algorithm that avoided areas of non-native vegetation, minimized elevation gradients within individual landscapes, and maximized the distance between landscapes. Elevation data for masking were obtained from the Shuttle Tomography Radar Mission data (Rabus et al. 2003) (<http://srtm.usgs.gov/>), and land-cover data were obtained from the MODIS-derived land-

cover product, also available from the Distributed Active Archive Center. These selection criteria reduced the impacts of irrigation, within-landscape topographic effects, and potential effects of auto-correlation between different landscapes. The individual landscapes had an average separation distance of 200 km and a topographic relief within a landscape of 600 m. We used a non-linear inverse distance-weighted rescaling to generate estimated monthly precipitation totals for each individual landscape. As the precipitation data were too coarse

to describe spatial variation within each landscape, this rescaling was used to generate an average monthly precipitation for each landscape. The alternative approach, interpolating the patterns, would poorly describe the fine-scale spatial variation in precipitation. As expected, because we were sampling across an east-west precipitation gradient (Fig. 1a), some autocorrelation was evident in patterns of EVI, however this was generally observed at distances  $< 100$  km.

For the 7-year time series of vegetation and precipitation, we separated the annual data into summer monsoon (day of year 180-300) periods and the remaining days were classified as non-monsoon or winter (day of year 301-179). We individually analyzed data from each season to derive several phenological variables for every pixel within each local landscape. As a check, the sensitivity of the results to the day chosen for each season date was evaluated for several patterns, and no qualitative differences in the results were observed. Several alternative approaches are available for describing remote-sensed phenological variables. Since most commonly used methods lead to substantial smoothing (Reed et al. 1994; Jonsson & Eklundh 2004; Pettorelli et al. 2005; Zhang et al. 2005, 2006; Archibald & Scholes 2007), and we were particularly interested in identifying the spatial variation in phenological patterns, we generated metrics not requiring such smoothing and used: peak greenness (maximum EVI within a season), maximum growth (maximum increase in EVI between sequential images within a season), timing of peak greenness, timing of maximum growth, and the time between maximum growth and maximum decline as an estimate of growing season length. The use of maximum growth as a phenological variable as opposed to a modeled budburst is both empirically tractable – detecting large differences is much easier than small differences – and has meaningful ecological interpretation (White et al. 1997; Pettorelli et al. 2005). We do not present patterns in maximum senescence rate as these are contained within the timing of growth and the growing season length. Our metrics include the three broad classes of metrics identified by Reed et al. (1994): value (peak greenness and maximum growth), timing (timing of peak greenness and maximum growth), and integrated (growing season length) classes. The resulting data describe the spatial pattern of five phenological metrics coupled with monthly precipitation totals for summer and winter seasons within 38 distinct 625-km<sup>2</sup> landscapes distributed throughout southern Arizona for 6 years (Fig. 1b).

### *Pattern analysis*

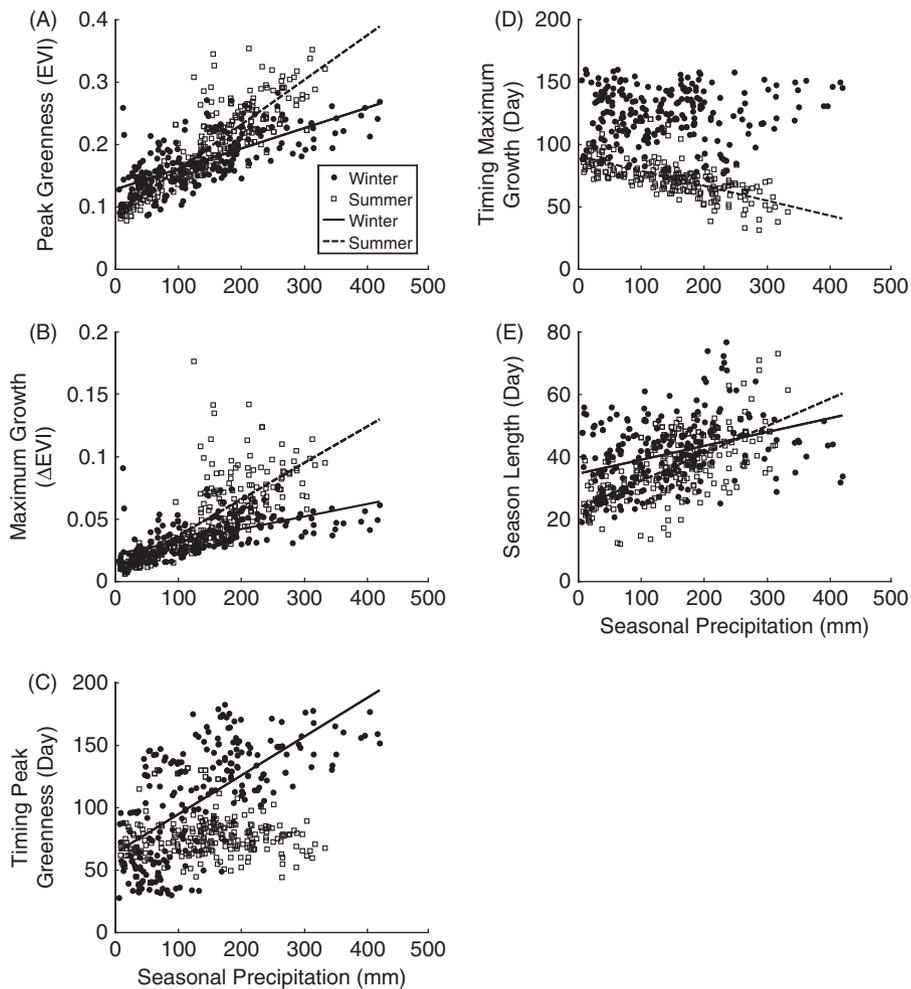
With the data described above, we examined the coupled variation between phenology and precipitation within and among different landscapes, between seasons, during individual years, and across multiple years. To identify mean effects of precipitation on phenological variation, each landscape and season combination was treated as an independent sample and linear regression was used to identify relationships between total precipitation and phenological variables. While several phenological patterns may respond non-linearly to precipitation, for example saturating functions may have a higher predictive value, we used linear approaches to efficiently test our hypotheses rather than specifically generating the best predictive model. We report only regression models where significant relationships ( $P < 0.05$ ) were identified. We evaluated the difference between winter and summer regression slope using an *F*-test (Sokal & Rohlf 1995). To estimate the effects of prior-season precipitation totals on phenological patterns, for each landscape we computed an independent linear regression model between total season precipitation and each phenological variable across all years. We then used linear regression to identify patterns between the residuals of these landscape-specific, within-season relationships to the total precipitation in the prior season. The slope of this relationship describes the effect of prior-season precipitation on current phenological dynamics after removing the effects of within-season precipitation. A positive slope would be evidence that prior-season precipitation increases a phenological variable above what was expected from the current-season precipitation alone, supporting the moisture-priming hypothesis. Differences between summer and winter responses to prior-season precipitation were assessed with a *t*-test.

Patterns of variation in phenology and precipitation were examined at four scales: (1) within-landscape and single season, (2) within-landscape and between seasons, (3) regional and single season, and (4) regional and multiple seasons. The total phenological variation, described as the coefficient of variation (CV), was computed within each landscape to assess landscape variation, among the landscapes to assess regional variation, or between years to identify inter-annual variation, and then this variation in phenology was related to precipitation variation (similarly estimated) for each scale using linear regression analyses. For the within-landscape and single-season scale, the spatial data

for precipitation were too coarse; at this scale we compared phenological variation to total season precipitation. To aid comparisons across scales, we also computed CV ratios between precipitation and phenology. Computing the CV ratio between phenological variation and precipitation relationships allowed for multiple-scale comparisons on relative phenological variation to precipitation. The application of CV ratios has become a useful tool for describing multiple-scale phenomena (Tilman et al. 1998; Jenerette et al. 2006) by providing a normalized description of relative variability between multiple groups.

## Results

Across landscapes, total annual precipitation ranged from 92 to 481 mm (mean 285 mm) and the proportion of precipitation arriving in winter varied between 39% and 77% (mean 51%). At the single-season landscape scale, the ranges of observed phenological variation and the direction of relationships were generally similar between summer and winter seasons (Fig. 2). Increases in within-season precipitation were associated with increases in peak greenness, maximum growth, and season length. For the timing of phenological patterns,

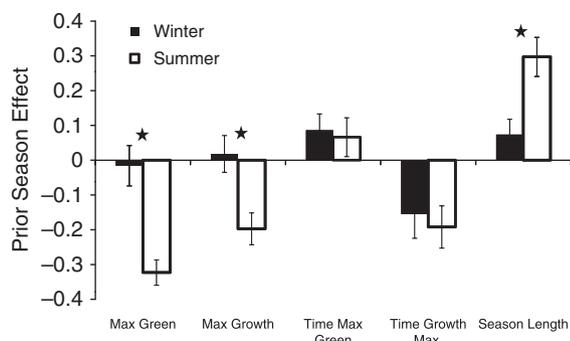


**Fig. 2.** Mean phenological responses assessed through changes in the enhanced vegetation index (EVI) to within-season precipitation for both summer and winter seasons at the individual landscape scale. Each point represents an individual landscape year. An  $F$ -test was used to determine if the slopes differed ( $df = 452$ ). (a) Peak greenness: winter (slope = 0.69;  $r^2 = 0.49$ ), summer (slope = 0.87;  $r^2 = 0.75$ ). The slopes do not differ ( $P > 0.1$ ;  $F < 1.0$ ). (b) Maximum growth: winter (slope = 0.62;  $r^2 = 0.38$ ), summer (slope = 0.75;  $r^2 = 0.56$ ). The slopes do not differ ( $P > 0.1$ ;  $F < 1.0$ ). (c) Timing of peak greenness: winter (slope = 0.66;  $r^2 = 0.43$ ), summer (NS). The slopes differ ( $P < 0.01$ ;  $F = 119.4$ ) (d) Timing of maximum growth: winter (NS), summer (slope = -0.65;  $r^2 = 0.42$ ). The slopes differ ( $P < 0.01$ ;  $F = 64.1$ ) (e) Season length: winter (slope = 0.37;  $r^2 = 0.14$ ), summer (slope = 0.65;  $r^2 = 0.42$ ). The slopes differ ( $P < 0.05$ ;  $F = 3.9$ ).

increases in rainfall resulted in either no effect or an advanced timing (i.e., earlier), which led to a positive relationship between total precipitation and season length. The magnitude of sensitivities and the degree of correspondence between value and integrated phenology metrics to total precipitation were similar across seasons. For phenological timing, the timing of peak greenness was insensitive to total precipitation in summer, while negatively related in winter; the timing of maximum growth was negatively related to total precipitation in the summer but insensitive in winter.

Prior-season precipitation totals were, in some cases, associated with the residual variation between phenological variables and within-season total precipitation (Fig. 3). Most strikingly, there were strong differences between summer and winter seasons associated with both peak greenness and maximum growth. Among all landscapes, these value metrics were not related to prior-season precipitation in winter, but were negatively related in summer ( $t$ -test,  $P < 0.05$ ). More winter precipitation was associated with reduced summer vegetation growth. For the timing and integrated phenological variables, summer and winter responded similarly to prior-season precipitation, delaying the time of maximum greenness, advancing the time of maximum growth, and extending the growing season ( $t$ -test,  $P < 0.05$ ). The effect of precipitation on growing season length was substantially larger during the summer than in the winter.

In contrast to the several clear patterns describing mean phenological patterns and precipitation at the individual season scale and inter-season connec-

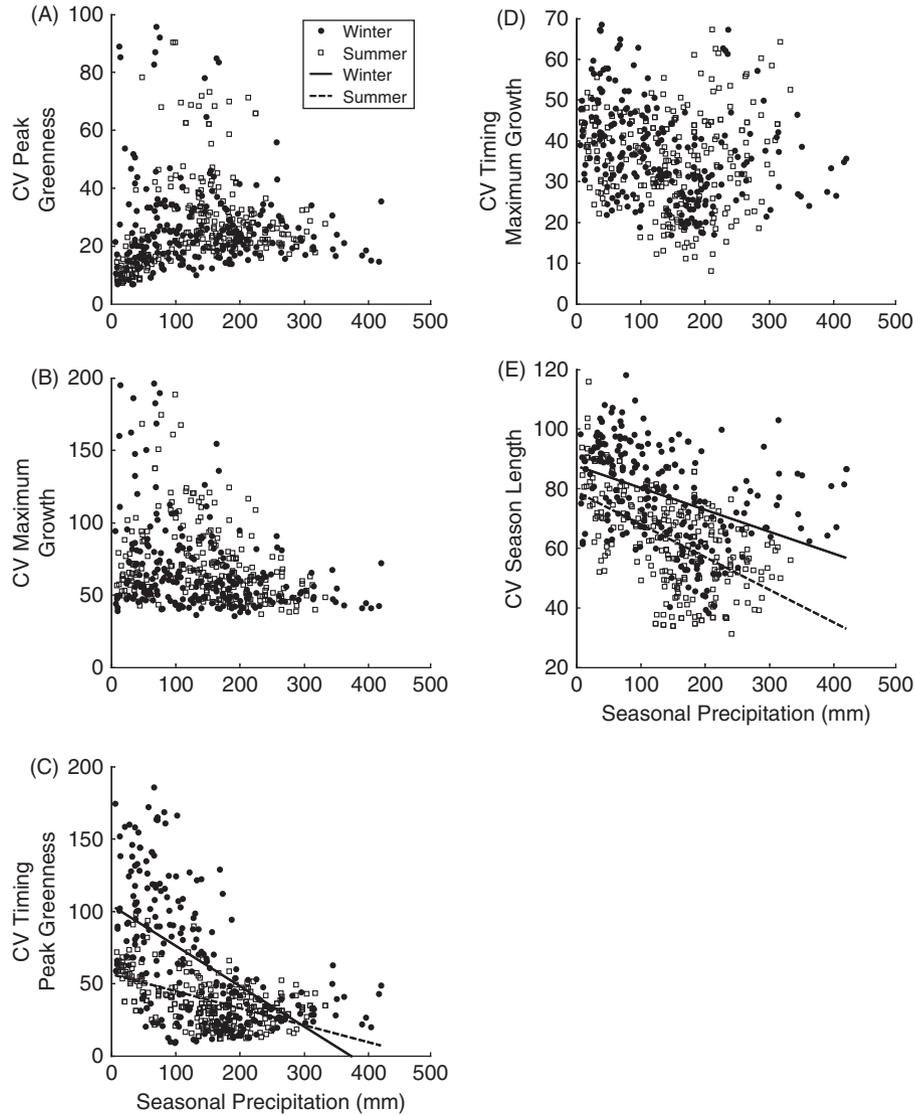


**Fig. 3.** Effects of antecedent precipitation on within-season precipitation phenological relationships. Antecedent effects were determined by first computing within-season phenology-precipitation regression, individually for each landscape, and then regressing the residuals of the first model to the amount of precipitation in the prior season. The mean and standard error of the slopes for the resulting effect of antecedent precipitation are shown for all landscapes. Stars above a winter-summer pair denote significant differences ( $t$ -test;  $P < 0.05$ ).

tions, relationships between the spatial variation of phenology and precipitation were less clear (Fig. 4). At single-landscape and individual season scales, precipitation amount was only related to the timing of peak greenness and growing season length. For both seasons, increases in precipitation were associated with decreases in within-landscape variability. Also, at this scale the magnitude of spatial variation within the landscape was similar between the two seasons.

At the regional and single-season scale, summer precipitation variation was larger than winter ( $t$ -test,  $P < 0.05$ ) and, similarly, regional variation in both peak greenness and maximum growth in the summer was larger than in winter ( $t$ -test,  $P < 0.05$ ). For timing and integrated phenological metrics, similar amounts of variation were observed in both summer and winter. There were no consistent differences between summer and winter phenological sensitivity to precipitation across all variables (Fig. 5). The CV ratio between precipitation and phenology showed peak greenness to be relatively more variable in summer than winter, while the timing and integrated season length variables were proportionately more variable in winter than summer ( $t$ -test,  $P < 0.05$ ). Seasonal phenological variability exhibited few relationships with precipitation variability in between-year analyses. Regional variation in peak greenness was positively associated with regional variation in precipitation during both summer and winter. Regional variation in maximum growth rate and timing of peak greenness were both positively associated with precipitation variability in winter and were insensitive in summer. In contrast, regional variation in the timing of maximum growth and season length were both positively associated with precipitation variability in summer, with no relationships identified in winter.

At the inter-annual and landscape scale, there were again no consistent phenological differences between summer and winter across all variables (Fig. 6). In contrast to the regional patterns of variation, in the temporal dimension precipitation was more variable for winter than summer ( $t$ -test,  $P < 0.05$ ). Inter-annual variation in peak greenness and timing of peak greenness were larger in winter than in summer, while the timing of maximum growth was more variable in summer ( $t$ -test,  $P < 0.05$ ). CV ratios between phenological and precipitation variability suggested all phenological metrics, except the timing of peak greenness, were proportionately more variable in summer than in winter. Evaluating the correspondence between inter-annual phenological variability with precipita-



**Fig. 4.** Phenological CV responses to within-season precipitation for both summer and winter seasons at the single season landscape scale. (a) Peak greenness: winter (NS), summer (NS). (b) Maximum growth: winter (NS), summer (NS). (c) Timing of peak greenness: winter (slope =  $-0.58$ ;  $r^2 = 0.33$ ), summer (slope =  $-0.52$ ;  $r^2 = 0.27$ ). The slopes do not differ ( $P > 0.1$ ;  $F < 1.0$ ). (d) Timing of maximum growth: winter (NS), summer (NS). (e) Season length: winter (slope =  $-0.41$ ;  $r^2 = 0.17$ ), summer (slope =  $-0.56$ ;  $r^2 = 0.31$ ). The slopes do not differ ( $P > 0.1$ ;  $F < 1.0$ ).

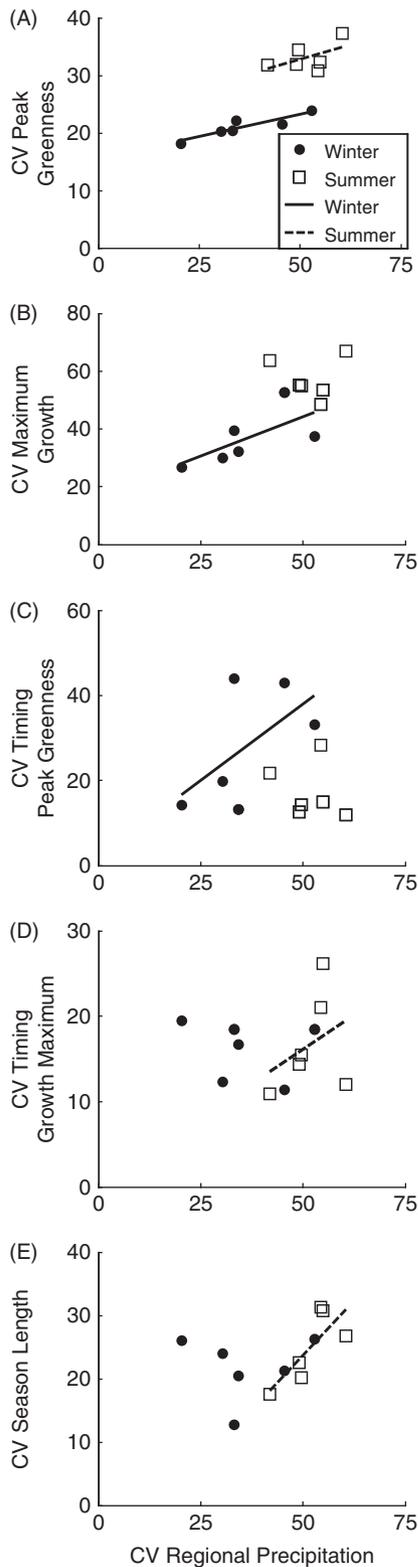
tion variability across landscapes again exhibited no consistent seasonal differences (Fig. 6). Inter-annual variations in peak greenness and maximum growth were positively related to precipitation variability in winter, while the timing of peak greenness and season length were positively related to precipitation variability in summer.

## Discussion

Vegetation patterns in southern Arizona were clearly coupled with precipitation variability – such

a coupling was not surprising. However, disaggregating phenological variation into value, timing, and integrated components (Reed et al. 1994) revealed complexity in precipitation-phenological relationships within and between growing seasons over multiple spatial and temporal scales. Hypothesized mechanisms of phenology-precipitation relationships (Table 1) were not consistently supported for all metrics across all scales. Phenology is multidimensional and scale-dependent. This complexity has often been difficult to characterize in water-limited regions (White et al. 1997; Archibald & Scholes 2007), and address-

sing interactions between precipitation and seasonality has been a noted key research need (Fang et al. 2005).



### Single-season individual landscape scale

At the single-season landscape scale, different hypotheses were supported for different aspects of phenological variation. Peak greenness and maximum growth rate in both summer and winter seasons responded positively to the amount of within-season precipitation (Fig. 2a and b), supporting a consistent water-use efficiency hypothesis across different rainfall inputs within a season. Similar relationships have been found in several other regions that have only a single growing season (Fang et al. 2005), and during the summer season in the Sonoran Desert (Cable 1975). In our study, winter and summer peak greenness were similarly responsive, suggesting the role of temperature-based metabolic activity in the summer that compensates for the reduction in effective rainfall associated with increased evapotranspiration and runoff.

In contrast to the value metrics, the timing (date of seasonal greenness peak and maximum growth) and season length metrics exhibited more complex responses. The timing of peak greenness showed strong differences between summer and winter seasons (Fig. 2c and d). Summer peak greenness timing was insensitive to the amount of rainfall, while winter peak greenness occurred earlier in seasons with more rainfall. Here, the summer patterns supported the state switches hypothesis and winter patterns supported a consistent water-use efficiency hypothesis. The timing of maximum growth patterns exhibited contrasting scaling patterns with precipitation between seasons – summer maximum growth occurred earlier with increasing rainfall, while winter maximum growth timing was insensitive to rainfall. These findings are not readily differentiable into either of the hypotheses proposed for winter and summer differences. Summer and winter growing season lengths again responded differently to increasing rainfall (Fig. 2e). Winter growing season length varied in a manner support-

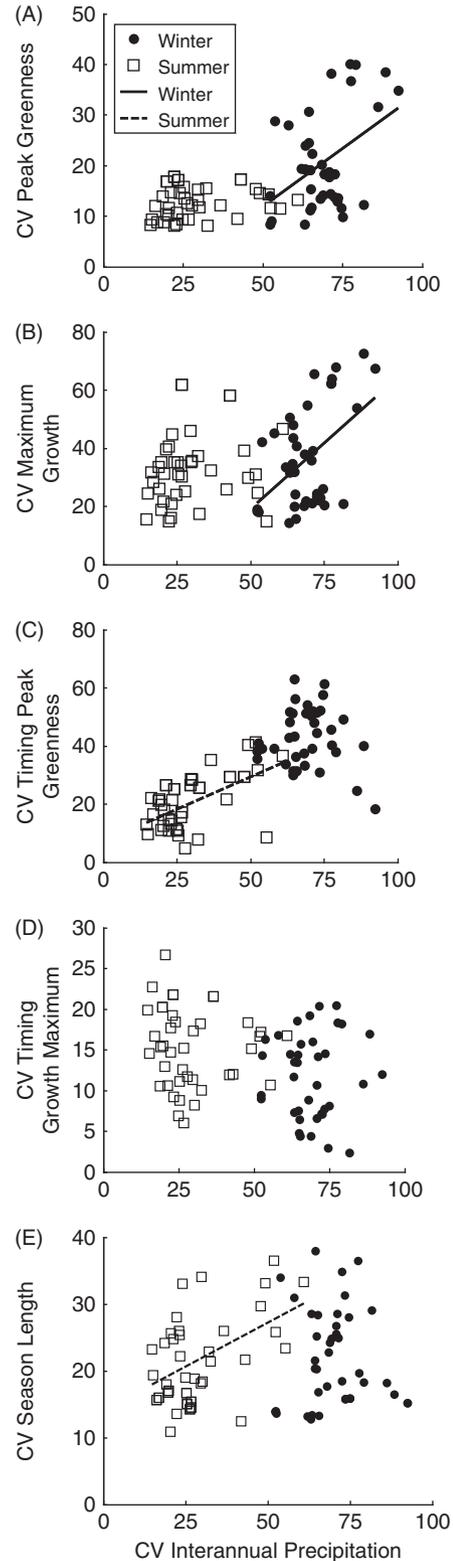
**Fig. 5.** Phenological CV patterns and precipitation for both summer and winter seasons at the single season regional (between landscape) scale. (a) Peak greenness: winter (slope = 0.91;  $r^2 = 0.83$ ), summer (slope = 0.54;  $r^2 = 0.30$ ). The slopes differ ( $P > 0.1$ ;  $F = 1.8$ ;  $df = 8$ ). (b) Maximum growth: winter (slope = 0.68;  $r^2 = 0.46$ ), summer (NS). The slopes differ ( $P < 0.01$ ;  $F = 31.0$ ). (c) Timing of peak greenness: winter (slope = 0.58;  $r^2 = 0.34$ ), summer (NS). The slopes differ ( $P < 0.01$ ;  $F = 13.0$ ). (d) Timing of maximum growth: winter (NS), summer (slope = 0.35;  $r^2 = 0.12$ ). The slopes differ ( $P < 0.05$ ;  $F = 5.4$ ). (e) Season length: winter (NS), summer (slope = 0.78;  $r^2 = 0.61$ ). The slopes differ ( $P < 0.01$ ;  $F = 31.5$ ).

ing the state switches hypothesis, while summer growing season supported a consistent water-use efficiency hypothesis. Again, these are not directly interpretable in terms of the hypotheses proposed to differentiate summer and winter seasonal precipitation responses. In answering our first question, total season precipitation was a key determinant of phenological values and season length for both summer and winter, while the responses of timing metrics were more variable. The lack of clear patterns in timing variables may be related to the coarse resolution of the PRISM data; previous studies have shown that timing of leaf-out may be most sensitive to the precise timing of precipitation inputs (Zhang et al. 2005).

*Phenological connections between seasons*

For the summer season, positive relationships between within-season precipitation and phenological value metrics were reduced with increasing previous-season rainfall, but no strong inter-season relationships were evident for winter phenology (Fig. 3). These findings support a functional separation of winter phenological response to summer rainfall and response of summer phenology to prior winter rainfall. In neither season was a priming effect observed on value variables. Three potential mechanisms for the inhibition effect on summer phenological response to current precipitation are plausible. First, the remaining biomass from the winter season could reduce the observed growth rate, although it is unclear how this would reduce summer total biomass. Second, prior-season precipitation could directly affect soil moisture at the beginning of the growing season – drier ecosystems may be more responsive to water inputs than wetter ecosystems (Wang et al. 2001; Huxman et al. 2004b). Third, inhibition could be related to nutrient availability – during years of substantial winter rains

and corresponding growth of winter vegetation, nutrients become immobilized in the newly decomposing biomass. Several recent studies have found strong interactions between nutrient and hy-



**Fig. 6.** Phenological CV patterns and precipitation for both summer and winter seasons at the inter-annual landscape scale. (a) Peak greenness: winter (slope = 0.44;  $r^2 = 0.15$ ), summer (NS). The slopes differ ( $P < 0.05$ ;  $F = 4.3$ ;  $df = 72$ ) (b) Maximum growth: winter (slope = 0.49;  $r^2 = 0.17$ ), summer (NS). The slopes differ ( $P < 0.01$ ;  $F = 31.0$ ). (c) Timing of peak greenness: winter (NS), summer slope = 0.58;  $r^2 = 0.33$ ). The slopes differ ( $P < 0.01$ );  $F = 13.0$ ). (d) Timing of maximum growth: winter (NS), summer (NS). (e) Season length: winter (NS), summer (slope = 0.48;  $r^2 = 0.23$ ). The slopes differ ( $P < 0.01$ ;  $F = 31.5$ ).

drologic cycles in water-limited systems (Hooper & Johnson 1999; Welter et al. 2005; Harpole et al. 2007). For both phenological timing variables and integrated season length, an antecedent priming effect of prior-season rainfall was found. In addition to these effects on the magnitude of phenology, increasing prior-season rainfall advanced the timing of maximum growth, delayed the timing of maximum greenness, and lengthened the growing season. Together, these findings suggest prior rain increases the active window – a priming of time – but decreases maximum growth. In answering our second question, the effects of prior-season rainfall are dependent on the season and variable between the phenological value and timing. Why this effect happened in summer and not in winter is unclear. The net effects of these differences on vegetation dynamics and whole ecosystem functioning are difficult to assess and remain an open research question.

#### *Inter-annual and regional scales*

Phenological patterns also varied at landscape, regional, seasonal, and inter-annual scales. Large differences were observed between within-landscape and regional variability. At the within-landscape scale and for individual seasons, the magnitude of phenological variation was comparable between summer and winter seasons (Fig. 4). This was surprising, as we had expected the spatially coherent frontal rains in winter to generate more homogeneous patterns than the more spatially variable summer convective storms. This finding supports the importance of other factors, likely soils or species differences, in shaping patterns of landscape-scale phenological heterogeneity (Park et al. 2004). At the regional (i.e., between landscapes) scale, summer phenological spatial variation was generally larger than that in winter. In contrast, at inter-annual temporal scales, winter phenological variation was generally larger than summer phenological variation. The differences between inter-annual and regional phenological variation were associated with similar differences in precipitation variation; summer regional variation was larger than in winter, while winter inter-annual variation was larger than in summer (Figs 5 and 6). In answering our third question, variation in phenological values between summer and winter differed at regional and inter-annual scales but not at individual landscape scales. However, if phenological variation was normalized by precipitation variability (i.e., CV ratio), then a more consistent pattern emerged, where summer

spatial variation was larger than winter spatial variation.

#### *Broader implications*

These findings have several implications for building more robust population, community, ecosystem, and land-surface understanding. The widely applied ecohydrological optimality hypotheses (Eagleson 1982; Scanlon et al. 2005) do not explicitly include phenological dynamics. Perhaps accounting for not only the amount of vegetation but the timing of vegetation activity could help resolve some of the problems associated with temporal variation in vegetation-hydrologic relationships (Kerkhoff et al. 2004). A comprehensive mechanistic modeling of the triggers for phenological events, such as leaf-out and senescence, has been elusive, especially in water-limited regions (White et al. 1997; Botta et al. 2000; Picard et al. 2005), although large strides are being made with more detailed treatments of hydrology (Jolly & Running 2004). In developing models of vegetation-climate interactions, a common approach separates vegetation into functionally distinct vegetation types (Pillar 1999; Schwinning & Ehleringer 2001); including phenological responses as one of the determinants of vegetation type is essential to the application of such approaches. Recent studies have suggested phenological patterns are correlated with other functional traits (Campagna & Bertiller 2008), and such linkages provide an organizing framework for extending the use of phenology in ecological models. The finding of a strong inhibitory effect of prior precipitation on phenology-precipitation relationships within the summer may be an important environmental relationship, which currently is not included in phenological models. The divergence between seasons in precipitation-phenology relationships identified here also suggests multiple models rather than a single, globally relevant description may be needed.

These results are particularly relevant for understanding vegetation responses to and interactions with global climate changes. Understanding the spatial and temporal patterns of vegetation variability often provides clues into likely future responses to global changes (Garbulsky & Paruelo 2004; Piao et al. 2004; de Beurs & Henebry 2005). Recent climate projections suggest substantial changes to the hydrologic cycle (Douville et al. 2002; Wentz et al. 2007), with more drought conditions predicted for the Sonoran Desert (Cook et al. 2004; Seager et al. 2007). Precipitation changes, in either total amounts or distribution between seasons, are

expected to generate several cascading biological responses, including changes to vegetation phenology (Penuelas et al. 2004; Cleland et al. 2007). Changes in phenology, as presented here, are often associated with changes in flowering, fruiting, and the production of seedlings (Penuelas et al. 2004), and will likely affect vegetation community assemblages. The direct effects of phenological changes and indirect effects through changes in species composition are also likely to affect terrestrial-atmospheric carbon exchanges and evapo-transpiration, and have consequences for vegetation feedbacks to climate changes (Epstein et al. 1999; Scott et al. 2006; Shen et al. 2008). These findings may be broadly relevant to other water-limited regions, which have been estimated to cover 35–45% of the global land surface (Asner et al. 2003; Reynolds et al. 2007). However, precipitation-phenology connections may be important for other regions – at the other hydrologic extreme in a wet tropical forest spatial scaling of satellite-observed greenness also exhibited strong relationships with precipitation (Poveda & Salazar 2004). By better describing recent patterns of vegetation phenology and its dependence on recent meteorology, we can begin to develop more mechanistic models of phenological trajectories in response to global changes.

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