Running head: Extreme event phenology

PHENOLOGY OF MIXED WOODY-HERBACEOUS ECOSYSTEMS FOLLOWING EXTREME EVENTS: NET CHANGES FROM DIFFERENTIAL RESPONSES

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Abstract. Ecosystem responses to key climate drivers are reflected in phenological dynamics such as the timing and degree of “green-up” that integrate responses over spatial scales from individual plants to ecosystems. This integration is clearest in ecosystems dominated by a single species or life form, such as seasonally dynamic grasslands or more temporally constant evergreen forests. Yet many ecosystems have substantial contribution of cover from both herbaceous and woody evergreen plants. Responses of mixed woody-herbaceous ecosystems to climate are of increasing concern due to their extensive nature, the potential for such systems to yield more complex responses than those dominated by a single life form, and projections that extreme climate and weather events will increase in frequency and intensity with global warming. We present responses of a mixed woody-herbaceous ecosystem type to an extreme event: regional scale piñon pine mortality following an extended drought and the subsequent herbaceous green-up following the first wet period after the drought. This example highlights how reductions in greenness of the slower, more stable evergreen woody component can rapidly be offset by increases associated with resources made available to the relatively more responsive herbaceous component. We hypothesize that such two-phase phenological responses to extreme events are characteristic of many mixed woody-herbaceous ecosystems.

Key words: phenology, piñon, dieoff, mortality, woody and herbaceous plants, drought, extreme events, disturbance, fire, semiarid woodlands, Mesita del Buey, Normalized Difference Vegetation Index

INTRODUCTION

Phenological studies in ecological systems focus on the timing and magnitude of recurring biological phases (phenophases), the influence of biotic and abiotic forces on timing, and the interrelation among phases of the same or different species (Post et al. 2007, Betancourt et al. 2005, Schwartz 2003). Scientifically important and societally relevant areas of investigation include how environmental factors affect phenophases (e.g., timing of vegetative vs. reproductive phases of the life cycle) for different organisms (Weiss et al. 1988, Both et al. 2007, Miller-Rushing and Primack 2007), how those factors vary in importance on different spatial and temporal scales (Lindblad and Molau 2007), and how phenology affects the abundance and diversity of organisms, including their function and interactions in the environment (Inouye 2007), and especially their effects on water, energy, and chemical fluxes at various scales (Kudo and Tanid 2007). Phenological responses are particularly significant when individual plant-level responses are intense enough to translate into whole-ecosystem responses. Perhaps most notably, the timing and degree of “green-up” are key ecosystem responses that reflect fundamental climate-vegetation couplings. Responses at ecosystem scales and greater (landscape, region, globe) are increasingly important to assess in the context of global warming (Chapin et al. 2000, Clark et al. 2001, Walther et al. 2002).

Phenological observation networks, such as the National Phenology Network, can provide valuable insight into ecosystem responses over large spatial scales (Schwartz 2003, Betancourt et al. 2005), and will be increasingly important as networks become more extensive and observations cover longer periods of time; however, currently the most effective means for assessing broad-scale ecosystem phenological dynamics is the use of satellite-derived remotely sensed data (Reed et al. 2003). Remotely sensed observations can provide a means to fill data gaps, both in terms of extensive spatial coverage and the ability to look back more than a decade. Among an increasing number of remotely sensed vegetation indices available to characterize primary productivity, we chose to use the Normalized Difference Vegetation Index (NDVI) because it has proven to be robust, reliable, and has been widely used to estimate regional patterns of primary productivity and biomass (Sellers et al. 1992, Wang et al. 2004, 2005), and because data from the National Oceanic and Atmospheric Administration's Advanced Very High Resolution Radiometer (NOAA/AVHRR) have been available continuously on a daily basis since 1989 as 1.1 km resolution composite images (Holben 1986). Indeed, the NDVI provides an integrated measure of productivity, with contributions from different plant functional types, and there is a growing body of research utilizing NDVI-derived plant phenological metrics for ecosystem monitoring (e.g., Potter et al. 1999, Tucker et al. 2001, Tateishi and Ebata 2004, White et al. 2005). The NDVI is calculated as the ratio of the difference over the sum of the near-infrared and visible reflectance values (Tucker 1979, Eidenshink and Faundeen 1994).

Although the emphasis of phenological research to date has often been on interannual variability in ecosystem responses to climate (Schwartz 2003), the largest changes in ecosystem and associated phenological patterns are likely to be associated with major ecosystem disturbances associated with extreme climate or weather events (Peñuelas and Filella 2001). Ecosystem disturbances, such as drought, fire, and hurricanes, modify phenological patterns of primary productivity (Knapp 1984a, 1984b, Johnson and Miyanishi 2007) via their impacts on species-specific performance, community structure, and the underlying resource base of water, solar radiation, and key nutrients needed for plant growth (Bloom et al. 1985). Long-term phenological impacts of such disturbances are expected to include ongoing shifts in the magnitude and timing of productivity resulting from restructuring of the community. Notably, extreme events are projected to increase in frequency with global warming (Easterling et al., 2000, IPCC 2001, Hoerling and Kumar 2004, Emanuel 2005, Trenberth 2005, Running 2006), which could trigger both short and long-term nonlinear, cross-scale impacts (Gutschick and BassiriRad 2003, Peters et al. 2004). For example, droughts in southwestern North America have triggered complex ecological responses associated with extensive tree mortality (Allen and Breshears 1998, Brown et al. 2001, Mueller et al. 2005), with implications for carbon balance (Breshears and Allen 2002, Kearns et al. 2005), plant water stress (Stimson et al. 2005), growth response (Fair and Breshears 2005), and host-pathogen and other symbiont interactions (Kearns and Jacobi 2005, Shaw et al. 2005, Mueller and Gehring 2006). Despite growing concern about the impact of extreme events on ecosystem dynamics, little phenological research has addressed this topic.

Climate-vegetation phenological relationships should be most temporally dynamic for systems that have a strong seasonality, such as a grassland or deciduous forest, relative to evergreen-dominated forest. As compared with evergreen woody species, herbaceous species tend to be more responsive to short-term climate fluctuations. For example, temperate evergreen woody species typically display relatively constant NDVI throughout the year, with only modest increases in summer in response to precipitation and warm temperatures; however, the NDVI for herbaceous species is usually relatively low in the winter, increases rapidly in the spring, and has distinctly high peaks in the summer (Harris et al. 2003). Although systems dominated by a single species or plant functional type are more readily interpretable in terms of effects of individual ramet response on whole ecosystem dynamics, a large portion of the terrestrial biosphere is actually intermediate between grassland and forest, having substantial amounts of cover from both herbaceous and woody plants (Breshears 2006). Predicting the dynamics of ecosystems with mixed woody and herbaceous components is particularly challenging given the complexity of interactions in mixed woody-herbaceous plant systems (House et al. 2003, Scanlon et al. 2005). These systems may be particularly sensitive, not only to climate variation, but also to extreme events and disturbances. Drought, fire, encroachment, wood harvesting, and grazing all alter the ratio of woody to herbaceous vegetation (Breshears 2006). Therefore, there is a critical need for studies that address net ecosystem phenological responses associated with shifts in community structure, such as recent widespread mortality of woody species in response to drought.

Collectively, responses of mixed woody-herbaceous ecosystems to climate are of increasing concern due to their extensive nature (House et al. 2003), the potential for such systems to yield more complex responses than those dominated by a single life form, and projections that extreme climate and weather events will increase in frequency and intensity with global warming. Here, we present a case study of phenological responses of a mixed woody-herbaceous ecosystem type to an extreme event. Our case study focuses on a semiarid woodland that had a nearly equal split in coverage between two evergreen woody plants—piñon and one-seed juniper (*Pinus edulis* and *Juniperus monosperma*, respectively)—and intercanopy areas, where the predominant herbaceous species was blue grama (*Bouteloua gracilis*). We report phenological and associated climatological conditions prior to, during, and following a severe extended drought (2000-2004) that resulted in mortality of most of the piñon trees in the ecosystem, thereby reducing the woody component substantially. More specifically, we quantify: i) variation in phenological and associated climatological variables during an eleven-year period prior to the severe regional drought; and ii) deviations from mean conditions in phenological variables during and following the drought. We use the seasonal variability in

NDVI as a metric of ecosystem phenology. Based on our case study and other related studies, we conclude by hypothesizing how ecosystems comprised of mixed herbaceous and woody evergreen ecosystems are expected to respond to different types of disturbances, noting expected similarities in two-phase phenological responses associated with both the woody and herbaceous components. More specifically, we argue that extreme events (e.g., drought, fire, hurricanes) lead to an initial depression of primary productivity, accompanied by a pulse of increased nutrient availability, which then leads to an increase in the importance of herbaceous plants, with a shift to greater variation in the overall ecosystem phenology and closer tracking of climatic variation, all of which is readily apparent in spatio-temporal analyses using remotely sensed vegetation indices. The greater amplitude of annual productivity variation is expected to continue for ecosystems that are significantly restructured toward greater importance of herbaceous plants, but may be more transient where the original structure is largely intact. Our case study builds on initial research in Breshears et al. (2005) that reported mortality of a single species (*P. edulis*), but that did not consider mixed woody-herbaceous interactions, and that preceded the compensatory response of intercanopy herbaceous vegetation presented here.

METHODS

We examined relations between environmental factors (temperature, precipitation, and soil moisture) and annual patterns of phenology (site NDVI and region NDVI) for an eleven-year baseline (1989-1999) and for five years since the onset of drought (2000-2004) at the Mesita del Buey long-term piñon-juniper woodland study site in northern New Mexico (Breshears et al. 1997). Daily maximum and minimum temperature and precipitation records from a nearby meteorological station were compiled as monthly mean temperature and monthly total precipitation. Soil moisture was measured one or more times per month using neutron attenuation (Rundel and Jarrell 1989) at 20 cm depth for eleven locations spaced at approximately 10 m intervals, and average monthly volumetric water content was calculated based on calibration for local soils.

Monthly values of NDVI from 1989 to 2004 at the site scale (based on mean weekly value for the 3 x 3 pixel window centered at Mesita del Buey) and at the region scale (based on mean weekly value for the area delineated as piñon-juniper woodland in the Gap Analysis Project 1:100,000 distribution map) were compiled based on techniques described by Breshears et al. (2005). NOAA-AVHRR NDVI composite data (maximum value technique to eliminate cloud contamination) were compiled and detrended by the Kansas Applied Remote Sensing Program (Kastens et al. 2003).

Herein we use the term phenograph to refer to the graphical depiction of the annual seasonal pattern of biological events and associated environmental factors. We constructed phenographs depicting monthly environmental and phenological metrics (mean temperature, precipitation, soil moisture, site NDVI, and region NDVI) at Mesita del Buey for each year of the baseline period (1989-1999), for the mean of the baseline period, and for the 95% confidence interval based on two standard deviations from the monthly mean. Phenographs for each year since drought onset (2000-2004) were constructed and compared to the baseline mean and 95% confidence interval. Site and region NDVI deviations from baseline were calculated on a monthly basis as the difference between a given year’s monthly value and the baseline mean, normalized by the standard deviation.

We calculated changes in canopy and intercanopy cover of the two major woody species (*P. edulis* and *J. monosperma*) at the Mesita del Buey site for the period since drought onset

(2000-2004) based on ongoing demographic inventories of survivorship and stand geometry measurements in a 50m x 50m mapped plot (Martens et al. 2000). Overlapping canopy cover for each woody species was estimated based on the number of stems observed for each species multiplied by the average crown radius (1.90 m for *P. edulus* and 1.15 m for *J. monosperma*, Martens et al. 1997) and divided by the mapped area. Non-overlapping canopy cover for each woody species was calculated based on the observed ratio of non-overlapping canopy to overlapping cover (43%:56%) measured in the mapped plot. Intercanopy cover was calculated as the complement of canopy cover (100% minus canopy cover). Herbaceous cover was scored at one cm intervals along a 100 m transect when the herbaceous canopy was at or near its peak development (July/August) during three of the baseline years (1995, 1997, and 1998) and during four of the years since drought onset (2001, 2002, 2003, and 2004).

RESULTS

Phenographs for the eleven baseline years at Mesita del Buey display tightly clustered temperature patterns and more highly variable patterns of other environmental and phenological metrics (Fig. 1). Mean temperature showed a peak in July (mean monthly temperature [t] = 20.69 °C, standard deviation [sd] = 0.69 °C) and a trough in January (t = -0.98 °C, sd = 1.72 °C) (Fig. 1A). Precipitation displays a small peak in May (t = 37.6 mm, sd = 26.4 mm), a larger peak in August (t = 76.9 mm, sd = 24.7 mm), and a trough in February (t = 16.8 mm, sd = 16.1 mm) (Fig. 1B). Soil moisture shows a peak in March (t = 25.0 %, sd = 6.6 %) and a broad trough in July (t = 16.4 %, sd = 1.5 %) (Fig. 1C). Mean site and regional NDVI display a rapid rise during May, a slight peak in June, a slight dip in July, a slight increase to a maximum value in September (site NDVI = 0.422, sd = 0.023; region NDVI = 0.398, sd = 0.029), a moderately rapid decline in the fall months. Minimum values for site (January site NDVI = 0.260, sd = 0.062) and region (February region NDVI = 0.2462, sd = 0.327) occurred one month apart (Figs. 1D and 1E). Winter NDVI values are often affected by snow, such that low values may result either from high snow levels or dry conditions with low green biomass.

Phenographs since drought onset (2000-2004) demonstrate significantly warmer temperatures, lower rainfall, and extensive periods of low soil moisture relative to baseline years (Figs. 2A, 2B, and 2C). Overall mean temperature during 2000-2003 (11.13 °C) is significantly higher than baseline (10.07 °C) (Student T test p = 0.0030, T = -3.636, df = 13). Mean temperatures were especially high during winter and spring of 2000, summer and early fall of 2001, spring and summer of 2002, and July 2003 (July t = 24.69 °C, 5.8 standard deviations above baseline), with temperatures nearer to baseline during 2004. Temperatures decreased during periods of higher rainfall (e.g., fall 2000 and 2002), presumably due to increased cloud cover.

Precipitation was generally below baseline during 2000-2003, except during 2000 (Fig. 2B). Mean annual precipitation during 2000-2003 (255.8 mm) was significantly lower than baseline (416.6 mm) (Student T test p = 0.0002, T = 5.236, df = 13). During 2004 precipitation (470.2 mm) was near baseline during winter, high during April (89.7 mm), low during May (0.25 mm) and June (19.30 mm), near baseline in July (65.0 mm) and August (50.3 mm), and high in October (82.8 mm).

Soil moisture started low in 2000 (~13% vs. baseline of 20-25%), increased to upper range of baseline during November 2000 through March 2001 (March peak = 33.8%), then declined to very low values (~13-14%) from mid-2001 through fall 2002 (Fig. 2C). This rise in soil moisture appears to relate to precipitation peaks during August and October 2000, with corresponding soil moisture peaks in December 2000 and March 2001 (December soil moisture = 28.8 %, March soil moisture = 33.8 %), with a lag of 4-5 months. Mean annual soil moisture during 2000-2003 (17.1%) was not significantly below baseline (19.2%) (Student T test p = 0.1549, T = 1.510, df = 13); however, mean soil moisture for July 2001 through October 2002 (13.7%) was significantly below baseline (19.2%) (Student T test p < 0.0001, T = 8.862, df = 25). During November 2002 through June 2003 soil moisture rose to near baseline (~20%), apparently in response to near baseline precipitation during late summer/fall 2002 and late winter/early spring 2003. Soil moisture declined again to low levels (~14%) during July 2003 through January 2004. Average 2004 monthly soil moisture (20.1%) was near baseline (19.2%), yet annual variability was different from baseline, with a peak in spring (May soil moisture = 32.0%), a decline during June through September (12-13%), and a rise to near baseline during October through December (December soil moisture = 23.4%).

Phenographs of site and region NDVI during the snow-free period (June through October) of 2000, 2002, and 2003 display low values (mean site NDVI = 0.366, deviation 1.4) relative to baseline (0.402), with recovery toward baseline during part of 2004 (Figs. 2D and 2E). During 2004 site NDVI follows the lower range of baseline. Near baseline NDVI was observed during winter 2001-2004 for the site and region; however, baseline years have low winter NDVI because of snow, whereas post-dieoff years have low NDVI because of decreased woody cover. Generally, site and region NDVI show similar phenological patterns, though regional values were less variable. Changes in NDVI are readily interpreted by examining NDVI deviation (Figs. 2F and 2G). Strong negative deviations at both local and regional scales occur during summer 2000 (June 2000 site deviation = -3.7, July 2000 site deviation = -3.8, August 2000 region deviation = -2.9). Strong negative deviations occur during summer and fall 2002 (site

September 2002 NDVI deviation = -5.8, July 2002 region negative deviation = -2.8), the period when most of the piñon mortality occurred. NDVI during 2003 and 2004 (Figs. 2D and 2E), while also low, generally increases, with 2004 values fluctuating between the lower baseline and the baseline mean for site NDVI, and around baseline mean for region NDVI. Overall, the phenological pattern shifted from low NDVI values during the early drought, to still lower NDVI values after the piñon dieoff event, then back toward the baseline during the post-dieoff period, yet with more variability than prior to the drought.

Non-overlapping woody cover decreased from 43.0% before the piñon dieoff event to 13.6%, with nearly complete loss of the piñon overstory canopy (Fig. 2H). At the same time, intercanopy cover increased from 57.0% to 86.4% (Fig. 2I). Herbaceous cover during 2001 (7.6%) and 2002 (3.3%) dropped below baseline (13.7%), rose above baseline during 2003 (18.9%), and rose still farther during 2004 (52.8%) (Fig. 2I). Subsequent to the mortality of more than 90% of *P. edulis* in the piñon-juniper woodland at the Mesita del Buey study site, we observed greatly reduced woody canopy cover, a corresponding increase in intercanopy cover, and a significant flush of herbaceous growth (Fig. 3).

DISCUSSION

Our baseline phenographs of climate variation and associated ecosystem response (Fig. 1) provide insight into three major categories of phenological behavior (Betancourt et al. 2005, Schwartz 2003). First, the baseline phenographs of NDVI at the site and regional scale, in combination with the associated temperature, precipitation, and soil moisture measurements, provide insight into the timing and magnitude of recurring biological phases associated with greenness and primary productivity. We observed similar patterns of NDVI response at site and regional scales, with similarities due to comparable overall response to prevailing climatic conditions, and with differences in the timing of greenness onset, peak, length of growing season, and senescence associated with the unique site climatic conditions and ecology (e.g., Wang et al. 2004). NDVI integrates greenness across all ecosystem components, and as such is a synoptic tool of overall system response. If used in conjunction with a continuous series of climatic and field measurements, NDVI can be used to elucidate both baseline ecosystem behavior, in terms of the timing and magnitude of green-up, and ecosystem changes in response to disturbance, in terms of changes in the timing and magnitude of green-up.

Second, the baseline phenographs provide insight into the causes of the timing of the phenophase of interest, particularly with regard to relations with variation in abiotic parameters. Notably, there is a distinct non-linear coupling between NDVI, soil moisture, and precipitation, such that site peak NDVI lags peak soil moisture, which in turn lags peak precipitation in winter, highlighting the fundamental importance of soil water in driving ecosystem dynamics. The baseline data also highlight that, although precipitation and soil moisture affect timing and magnitude of peak NDVI, peak precipitation is not the factor driving these dynamics. Peak precipitation occurs midsummer in conjunction with peak temperature, and hence high evaporative demand leads to reduced plant-available water (Loik et al. 2004). In general, our baseline phenographs are consistent with an understanding that precipitation and temperature together drive soil moisture, which in turn drives productivity.

Third, the baseline phenographs provide insight into the interrelation among phases of same or different species. In the case of mixed woody-herbaceous systems such as piñon-juniper woodlands, the woody plants respond relatively slowly, contribute to a background NDVI year round, and modestly track ideal growing conditions defined by temperature and water availability; however, herbaceous plants respond quickly, contribute to more dynamic seasonal changes in NDVI, and more closely track optimal growing conditions. The baseline phenographs provide insight into the overall ecosystem responsiveness to climatic variation, but alone do not permit us to distinguish interactions and relative contributions of woody versus herbaceous plant functional types. Rather they provide the reference against which to measure changes, in our case the effect of an extreme event: drought-induced tree mortality, with major reduction in woody canopy providing a natural experiment to understand the interaction between woody and herbaceous components of the system.

Thus, the baseline phenographs provide both useful understanding of the basic functioning of the piñon-juniper woodland and the reference against which to measure change, and highlight how climatic variance associated with precipitation is much greater than that associated with temperature. Soil moisture integrates the precipitation and temperature drivers and translates them into ecosystem responses as measured by NDVI. The results also highlight important year-to-year differences. Generally years with higher precipitation had higher soil moisture and higher NDVI; higher winter precipitation led to a more marked green-up, and when accompanied with large monsoonal rains, led to a higher peak NDVI. Overall, the results highlight the utility of solid, decadal-scale data on phenology and associated climatic patterns. Baseline data of this type are needed to address a diverse set of ecological issues, from understanding dryland degradation (Breshears et al. 1997), changes in keystone processes such as fire (Swetnam et al. 1999), and restoration of a diverse set of ecosystem types (Hobbs and Norton 1996, Hobbs and Harris 2001, Falk et al. 2006). Continuous long-term data such as these provide the basis for improved understanding of, and in some cases mitigating, the impacts of disturbances that can be characterized as extreme events. Disturbances of this kind include fire, drought, hurricanes, and defoliating hail storms. Extremely wet years can also be viewed as a type of disturbance, as they have the potential to shift many ecological aspects of the system.

Phenographs for the period since onset of drought (Fig. 2), as compared with the site baseline, give insight into ecosystem impacts of extreme events. NDVI during the drought was often near or beyond the extremes of the pre-drought baseline patterns, which is particularly clear when temporally specific deviations are evaluated (e.g., Figs. 2F and 2G). The major reduction in NDVI in 2002 corresponds to the onset of massive piñon mortality. Detecting such large declines may be particularly important for monitoring vegetation response to climate variability and change at landscape to regional scales. The reduction in NDVI associated with piñon mortality is more clearly understood when the temporal dynamics of the baseline are considered, as they were here, than when simply evaluating variation against a long-term annual mean, as has been done previously (Breshears et al. 2005). In particular, our current analyses demonstrate a very interesting and somewhat surprising result: soon after the first major soil water input following the tree mortality there was a substantial green-up of vegetation due to the smaller but more responsive herbaceous component (Fig. 2I), as is clearly visible in Fig 3.

Large portions of intercanopy areas that were bare and patches under trees that died are likely to have more biologically available water, nutrients, and solar radiation following the tree mortality event (Loik et al. 2004, Breshears et al. 1997); therefore, there was a rapid herbaceous response that effectively returned the system to NDVI levels similar to those prior to the drought. It is unlikely that the system has returned back to pre-mortality levels of biomass, but because herbaceous vegetation can expand and cover previous non-green areas under the woody canopy, the overall system response in terms of greenness that was reduced by loss of woody plants, was quickly compensated for by an increase in herbaceous plants.

Hence, what is particularly interesting about the response of the mixed woody-herbaceous system to drought is not simply that there was a threshold combination of drought duration and intensity that triggered tree mortality, but also that there was a rapid recovery with respect to ecosystem productivity, due largely to herbaceous responsiveness. These dynamics highlight the fundamental coupling between woody and herbaceous plants in these mixed systems, and the degree to which changes in one of the two plant functional types can be offset by changes in the other (House et al. 2003, Breshears and Barnes 1999, Walker 1987). In essence, this interaction involves an extreme event or disturbance that greatly reduces the evergreen woody canopy, yet at the same time makes resources available, and is followed by rapid herbaceous growth. Although there is an apparent compensation in which NDVI is tending to return to pre-drought levels, we expect to observe a different pattern of phenology, given that woody plant cover is now greatly reduced and that intercanopy area is proportionately increased (Figs. 2H and 2I). In general, we expect that the ecosystem will more closely track climatic conditions, with greater senescence during the winter due to the sparcity of the evergreen woody canopy, and greater green-up in the summer due to greater green-up of herbaceous plants and more rapid response to growing season precipitation events and temperature variability.

In general, we hypothesize that extreme events will impact mixed woody-herbaceous ecosystem phenology, first by a depression in productivity, followed by a flush of productivity as resources are made available (Fig. 4A). For extreme events that involve extensive mortality of woody species, as is the case for drought-induced tree mortality, fire, and hurricanes, this change is expected to be persistent, with a lower winter baseline, higher peaks, and generally greater responsiveness to climate conditions (Figs. 4B and 4C). For example, after fire ecosystem primary productivity is typically dominated by the successional herbaceous community (Johnson and Miyanishi 2007). In contrast, in cases where there is no significant woody mortality, for example short droughts and defoliation due to hailstorms or herbivores, we expect only a transient response, with phenological patterns of productivity quickly approaching baseline levels (Figs. 4D and 4E). Similarly, extremely wet years can be viewed as extreme events that only produce a transient effect (Fig. 4F). Thus, we hypothesize a general two-phase pattern of response to extreme events, with a transient phase of depressed NDVI followed by a recovery phase to either near normal or elevated conditions. This two-phase response can be thought of as a phenological signature that distinguishes the temporal dynamic of ecosystem response to many extreme events.

CONCLUSION

Developing a solid understanding of baseline phenology, including synoptic remote sensing measures such as NDVI, is fundamental to understanding ecosystem function, and serves as a reference against which to measure change. To date, much of our understanding of ecosystem phenology has focused on subtle year-to-year shifts for specific study sites. However, larger shifts across broad geographic areas, for example those associated with extreme events, can reshape ecosystem structure and reset trajectories such that phenological patterns are fundamentally altered for long periods of time.

Similarly, much of basic phenological research has focused on relatively homogeneous ecosystems, in part because mixed systems are more difficult to track. Our results suggest a tractable approach to understanding ecosystems that contain two major plant functional types—woody and herbaceous species. Responses of mixed woody-herbaceous ecosystems to climate are of increasing concern due to their extensive nature, the potential for such systems to yield more complex responses than those dominated by a single life form, and projections that extreme climate and weather events will increase in frequency and intensity with global warming.

The example of drought-induced tree mortality followed by a flush of herbaceous growth highlights how reductions in greenness of the slower, more stable evergreen woody component can rapidly be offset by increases associated with resources made available to the relatively more responsive herbaceous component. We hypothesize that such two-phase phenological responses are characteristic of many extreme events and characteristic of many mixed woody-herbaceous ecosystems.

Our study contributes to a growing body of phenological research that illuminates fundamental ecological responses to climate. This Special Issue illustrates the breadth, depth, and growing recognition of the importance of phenology, especially in the context of global warming and increasing climate variability (Both et al. 2007, Inouye 2007, Kudo et al. 2007, Miller-Rushing and Primack 2007, Post et al. 2007). These phenological responses are manifest in a variety of ways, originating at ecophysiological scales and expressed through individual organisms, populations, communities and, notably, at landscape and regional scales. Our results build on previous and emerging advances in phenology and highlight the complexity of broad scale phenological responses to extreme climatic events for mixed woody-herbaceous ecosystems. We expect dramatic shifts in ecosystem phenology, triggered by extreme climatic events, to become increasingly prevalent as climate change progresses.

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FIGURE LEGENDS

Figure 1. Baseline phenographs depicting monthly environmental and phenological metrics at Mesita del Buey study site in northern New Mexico: A) mean temperature, B) precipitation, C) soil moisture, D) site NDVI, and E) region NDVI. Gray curves represent each year of the eleven-year baseline period (1989-1999), the solid dark curve displays the mean monthly values during the baseline period, and the dashed dark curves demark the 95% confidence interval (2 standard deviations from the mean).

Figure 2. Phenographs for each year since drought onset (2000-2004), depicting monthly environmental and phenological metrics at Mesita del Buey. For each plot, the metric of interest is illustrated with a solid dark line, and the baseline mean (solid gray line) and 95% confidence interval (dashed gray line and associated gray area) are displayed for reference. Metrics include A) mean temperature, B) precipitation, C) soil moisture, D) site NDVI, E) region NDVI, F) site NDVI deviation from the baseline mean, G) region NDVI deviation from the baseline mean, H) canopy cover of piñon pine (*P. edulis*) and one-seed juniper (*J. monosperma*), I) intercanopy and herbaceous cover (closed circles depict the observed value for the particular year and open circles depict the mean baseline value for 1995, 1997, and 1998).

Figure 3. Photograph illustrating the flush of herbaceous growth in July 2004 at Mesita del Buey after more than 90% of piñon pine (*P. edulis*) died during 2002-2003 due to drought stress. Note the standing dead piñon pines and the living one-seed junipers (*J. monosperma*).

Figure 4. Theoretical framework for phenological responses to extreme events in mixed woody-herbaceous ecosystems. A) Dynamic interaction between climate drivers (precipitation and temperature) and primary productivity during pre- and post-extreme event conditions. Extreme events such as B) extended drought and C) fire display an initial depression in productivity after the extreme event, a flush of herbaceous productivity, and then a new phenological pattern with greater variation. By contrast, transient events that do not involve major loss of woody cover, such as D) a short drought, E) defoliation, and F) a very wet year, are only expected to show a short-term phenological change.

Figure 1

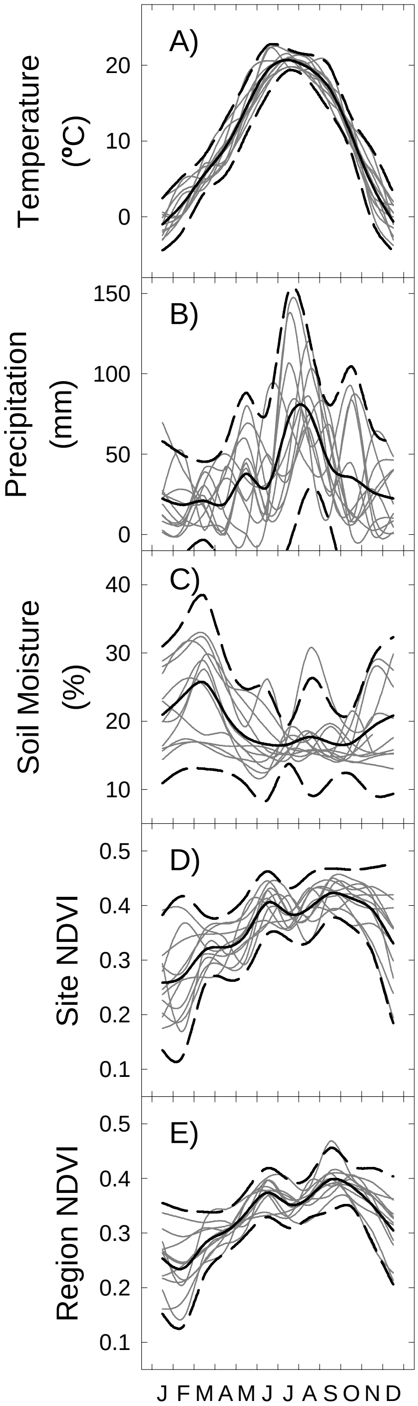
A)
Temperature (ºC)
20
10
0
B)
Precipitation (mm)
150
100
50
0
C)
Soil Moisture (%)
40
30
20
10
D)
Site NDVI
0.5
0.4
0.3
0.2
0.1
E)
Region NDVI
0.5
0.4
0.3
0.2
0.1
J F M A M J J A S O N D

Figure 2

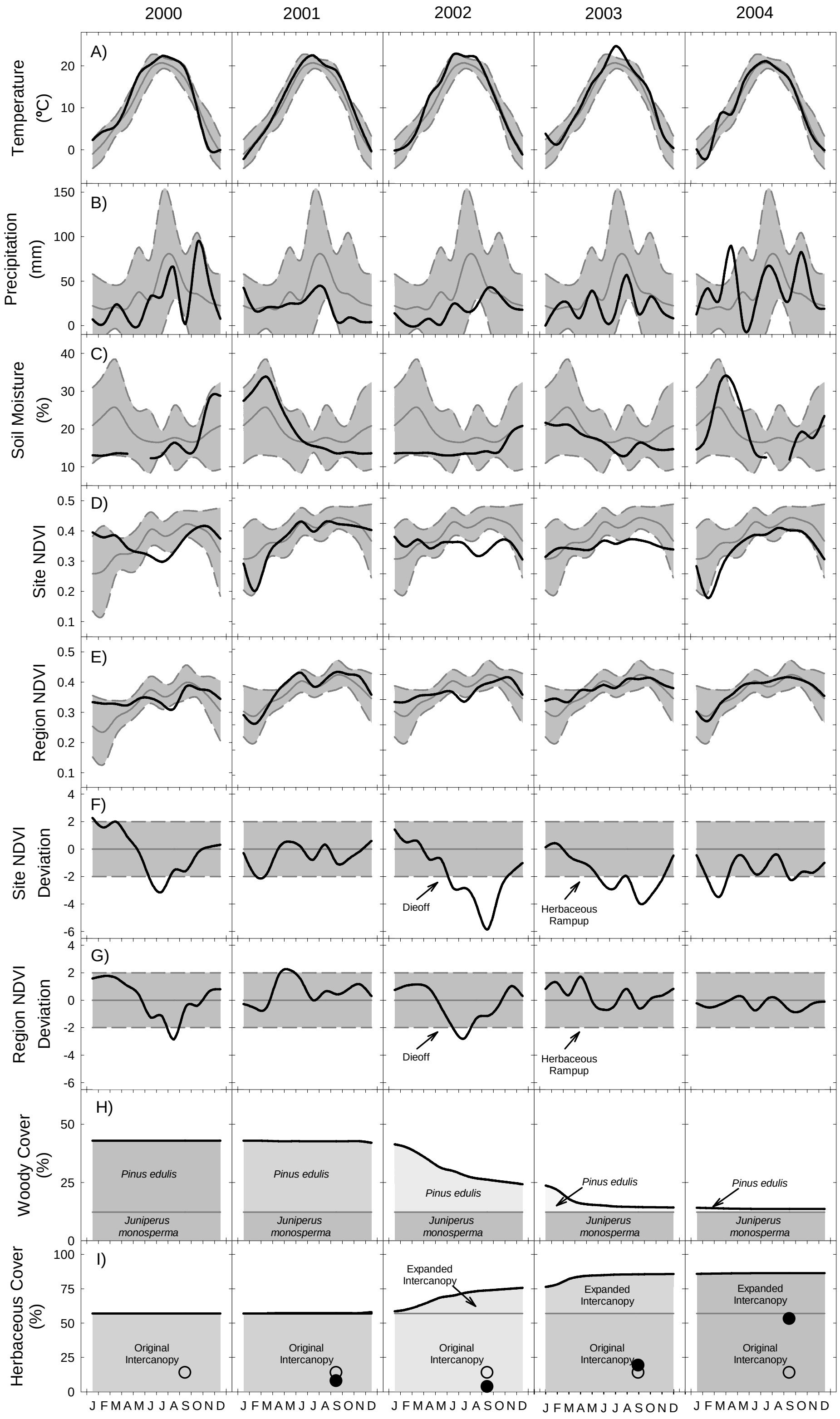
2000
2001
2002
2003
2004
A)
Temperature (ºC)
0
10
20
B)
Precipitation (mm)
0
50
100
150
C)
Soil Moisture (%)
10
20
30
40
D)
Site NDVI
0.1
0.2
0.3
0.4
0.5
E)
Region NDVI
0.1
0.2
0.3
0.4
0.5
F)
Site NDVI Deviation
-6
-4
-2
0
2
4
Dieoff
Herbaceous Rampup
G)
Region NDVI Deviation
-6
-4
-2
0
2
4
Dieoff
Herbaceous Rampup
H)
Woody Cover (%)
0
25
50
Pinus edulis
Juniperus monosperma
I)
Herbaceous Cover (%)
0
25
50
75
100
Original Intercanopy
Expanded Intercanopy
J F M A M J J A S O N D

Figure 3

Figure 4