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RESEARCH PAPER

Ecological consequences of variation in precipitation: separating short- versus long-term effects using satellite data

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ABSTRACT

Aim Precipitation controls the production of semi-arid plants through various mechanisms that operate at a range of time-scales. Short-term variation in precipitation affects vegetation through adjustments in plant physiology and leaf phenology, whereas long-term effects are mediated by plant establishment and mortality, community composition and disturbance regimes. Our goal is to use remote sensing observations to separate the short- and long-term effects of variation in precipitation on ecosystem production.

Location California, USA.

Methods We used time series of gridded absorbed photosynthetically active radiation (APAR) to quantify the short- and long-term responses of diverse ecosystems to variation in precipitation across large productivity and precipitation gradients. We investigated the relationships between temporal sensitivity of APAR to interannual variation in precipitation and mean annual precipitation (MAP), ecosystem properties and disturbance.

Results APAR increased with precipitation both interannually within locations and across locations with MAP. The slope of the interannual relationship, which reflects the sensitivity of APAR to short-term fluctuations in precipitation, varied with climate, vegetation type and structure, and time since disturbance. The interannual APAR sensitivity decreased from *c.* 0.5 MJ m^{-2} mm^{-1} at a MAP of 300 mm $year^{-1}$ to less than 0.05 MJ m^{-2} mm^{-1} at 1000 mm $year^{-1}$. The slope of the spatial relationship, which reflects the long-term sensitivity of APAR to climate, decreased from *c.* 2.5 MJ m^{-2} mm^{-1} at 300 mm $year^{-1}$ MAP to *c.* 0.6 MJ m^{-2} mm^{-1} at 1000 mm $year^{-1}$. The initial physiological and leaf area effects of a precipitation shift were amplified five-fold over time by gradual changes in population density and species composition.

Main conclusion The impact of a hydroclimatic shift on the primary production, structure and function of California's terrestrial ecosystems depends heavily on time-scale and how rapidly changes in plant population density and community composition can occur.

Keywords
Absorbed photosynthetically active radiation, ecological gradient, ecosystem functioning, grassland, gross primary production, MODIS, rain use efficiency, remote sensing, satellite observations, shrubland.

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INTRODUCTION

Water availability exerts a strong control over net primary production (NPP) in arid and semi-arid regions, regulating the year-to-year variation in NPP within individual sites and shaping the long-term distribution of NPP across the landscape (Knapp & Smith, 2001; Zavaleta *et al.*, 2003; Harpole *et al.*, 2007; Hsu *et al.*, 2012; Ruppert *et al.*, 2012). Climate models predict

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reduced precipitation and a drier climate throughout much of the semi-arid south-western United States by the mid to late 21st century, underscoring the need to better understand the sensitivity of semi-arid vegetation to changing precipitation (Hayhoe *et al*., 2004; Seager *et al*., 2007; Cayan *et al*., 2010).

Predictions of the impact of change in precipitation on vegetation are complicated by the wide diversity of biological mechanisms that may mediate the response (Smith *et al*., 2009; Williamson *et al*., 2012). Relatively short-term fluctuations in water input, associated with seasonal or interannual variation in precipitation, affect plant production through rapid adjustments in plant physiology, phenology, leaf growth and crown expansion or dieback (Penuelas *et al*., 2004; Zhang *et al*., 2005). Comparatively long-term shifts in water input, associated with climate variation, affect plant production through gradual changes in plant establishment and mortality, population density and species composition, disturbance regime and soil development (Kratz *et al*., 2003; Suttle *et al*., 2007). A clear distinction between the implications of short- versus long-term change in precipitation, and an improved understanding of the amplitude and reversibility of rapid versus gradual ecological response, are needed to anticipate the ecological consequences of climate change (Easterling *et al*., 2000; Walther *et al*., 2002; Smith *et al*., 2009).

Ecologists and biogeographers often use the temporal variation within a location to quantify the rapid physiological controls on ecosystem structure and function, and the spatial variation within or between biomes to identify the gradual, climatic controls (Goward & Prince, 1995; Knapp & Smith, 2001; Kratz *et al*., 2003; Huxman *et al*., 2004; Guo *et al*., 2012). Both *in situ* and remotely sensed satellite observations of vegetation structure show that ecosystem production is positively correlated with mean annual precipitation across spatial climate gradients (Leith, 1975; Goward & Prince, 1995; Yang *et al*., 2008). Similarly, productivity in arid and semi-arid environments often responds positively to interannual variation in precipitation, though the relationship is typically much weaker than that observed spatially (Sala *et al*., 1988; Knapp & Smith, 2001; Huxman *et al*., 2004). The rapid, temporal response of production to variation in precipitation within individual grassland sites is much weaker than the spatial relationship across grassland sites (Lauenroth & Sala, 1992; Sala *et al*., 2012). The temporal sensitivity also differs substantially among biomes, with the weakest response found in forest ecosystems and strongest in the herbaceous biome (Knapp & Smith, 2001; Huxman *et al*., 2004).

Observations over both extended time periods (at least 5 to 10 years; Baldocchi, 2001; Ito *et al*., 2005) and large spatial climate gradients are needed to investigate the productivity effects of short- versus long-term variation in precipitation. *In situ* observations of primary production, such as those collected by harvest, biometry or eddy covariance, can be used for this purpose (Zavaleta *et al*., 2003; Padgett *et al*., 2009; Sala *et al*., 2012). Net primary production has been measured at more than 500 locations globally, but most of these records are brief (Huxman *et al*., 2004; Padgett *et al*., 2009; Hsu *et al*., 2012), and the longer time series (> 10 years) are usually for grassland (Guo *et al*., 2012; Hsu *et al*., 2012; Sala *et al*., 2012). This lack of data has limited our understanding of how and why the short- and long-term effects of variation in precipitation differ between ecosystem types. Satellite remote sensing provides an alternative, highly efficient tool for monitoring vegetation activity at multidecadal time-scales and large spatial scales.

California, with its diverse ecosystems (Fig. 1a) and large geographic variation, provides an ideal test bed for further exploring the rapid, interannual and gradual, climatic controls on ecosystem productivity. Precipitation in California has large interannual, interdecadal, latitudinal and topographic variation (Fig. 1b) (Farrara & Yu, 2003; Pan *et al*., 2011), and terrestrial NPP is thought to be limited most strongly by drought and the lack of moisture (Barbour *et al*., 2007). We used 24 years of Advanced Very High Resolution Radiometer (AVHRR) satellite data and 11 years of Moderate Resolution Imaging Spectroradiometer (MODIS) data to derive gridded information on ecosystem function throughout California. We then combined these observations with gridded precipitation information to examine the spatial and temporal variability of satellite-derived vegetation productivity across California. We hypothesized that: (1) interannual variation in precipitation has a smaller effect on plant production, as defined by δNPP/δPrecipitation, than climatic variation in precipitation (Lauenroth & Sala, 1992; Goward & Prince, 1995; Huxman *et al*., 2004), and (2) the magnitude of response to interannual variation in precipitation differs in predictable ways with historic variability in precipitation, plant structural type, plant diversity and time since disturbance (Knapp & Smith, 2001).

MATERIALS AND METHODS

Satellite datasets: normalized difference vegetation index, fraction of absorbed photosynthetically active radiation (PAR), and PAR

We used the annual cumulative absorbed photosynthetically active radiation (APAR) as a proxy for plant production. APAR was calculated as the product of photosynthetically active radiation (PAR) and the fraction of PAR absorbed by plant canopies (fPAR). Annually integrated APAR is a measure of the total photosynthetically active photons absorbed by green leaves, and is closely linked with NPP and gross primary production (GPP) (Field *et al*., 1995).

The MODIS fPAR data set has been available since 2000 (Myneni *et al*., 2002), but lacks observations for barren and sparsely vegetated desert areas, which cover 22% of California's land surface. Hence, we derived fPAR from satellite observations of the normalized difference vegetation index (NDVI). NDVI is a robust, empirical measure of vegetation cover, which has been widely used for spatial and temporal comparisons of terrestrial photosynthetic activity (Trujillo *et al*., 2012). We used the MODIS NDVI data at 500-m resolution and 16-day intervals from 2000 to 2010 (Huete *et al*., 2002), and also the Global Inventory Modeling and Mapping Studies (GIMMS) NDVI

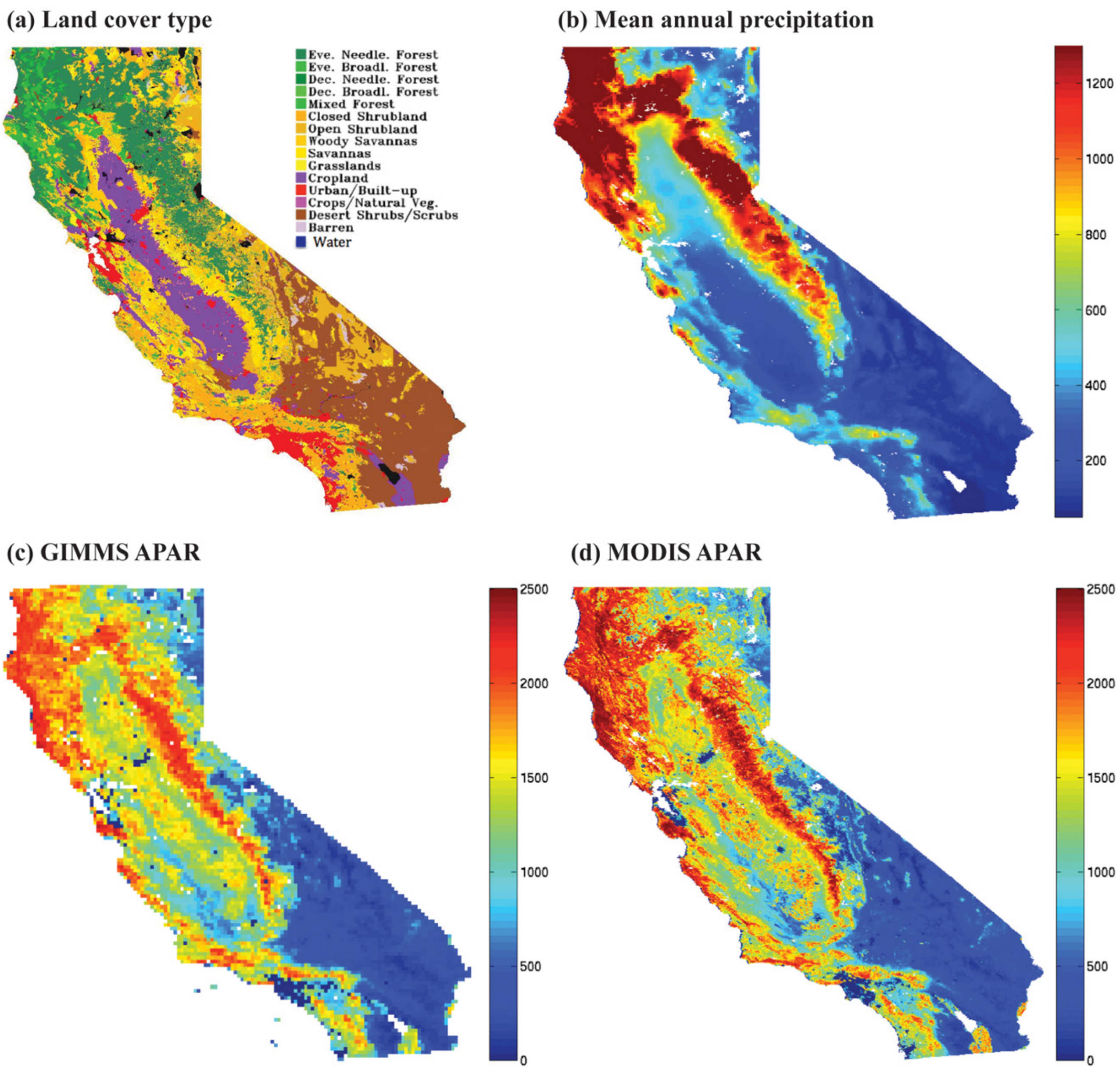

Figure 1 Distribution of (a) land cover across California, (b) mean annual precipitation during 2001–10 (mm year^{-1}), (c) absorbed photosynthetically active radiation (APAR; MJ m^{-2} year^{-1}) during 1983–2006 derived from the Global Inventory Modeling and Mapping Studies (GIMMS) data set, and (d) APAR during 2001–10 derived from Moderate Resolution Imaging Spectroradiometer (MODIS) observations.

dataset, based on AVHRR observations at 8-km resolution and 15-day intervals, for longer time-series analyses from 1982 to 2006 (Los *et al*., 2000; Tucker *et al*., 2005).

We used Los *et al*.'s (2000) approach to calculate fPAR separately from each NDVI dataset. The 98th and 2nd percentile values were determined from NDVI frequency distributions, and tied to a maximum fPAR value of 0.95 and a minimum fPAR value of 0.001, respectively. fPAR was then calculated as:

$$\mathrm{fPAR} = \frac{\mathrm{NDVI} - \mathrm{NDVI}^{\mathrm{min}}}{\mathrm{NDVI}^{\mathrm{range}}} \times \mathrm{fPAR}^{\mathrm{range}} + \mathrm{fPAR}^{\mathrm{min}}.$$

To derive MODIS-based APAR, we used the incident PAR dataset from the Global Energy and Water Cycle Experiment (GEWEX) Americas Prediction Project (Pinker *et al*., 2003) at 0.5° × 0.5° spatial resolution and a monthly time step from 1996 to 2010. Another monthly PAR dataset at 1° × 1° resolution from the Langley Surface Radiation Budget project from 1983 to 2007 was used for GIMMS-derived APAR (http://eosweb.larc.nasa.gov/PRODOCS/srb/table_srb.html) (Stackhouse *et al*., 2011).

Our APAR observations provided an excellent proxy for primary production. The annual APAR derived from remote sensing was well correlated with contemporaneous *in situ*

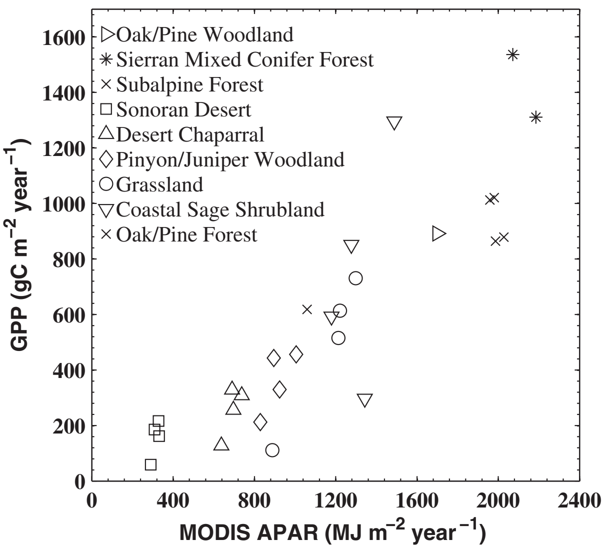

Figure 2 Annual gross primary production (GPP; gC m^{-2} year^{-1}) calculated by integrated eddy covariance as a function of the contemporaneous absorbed photosynthetically active radiation (APAR; MJ m^{-2} year^{-1}) based on Moderate Resolution Imaging Spectroradiometer (MODIS) observations. The eddy covariance observations were made at 10 sites in southern California and the Sierra Nevada (see Table S1 and Goulden *et al.*, 2012 for site details).

observations of GPP from eddy covariance towers across 28 site years (Table S1 in Supporting Information and Fig. 2; $R^2 = 0.78$) (Goulden *et al.*, 2006). The flux observations were made at 10 Californian sites that spanned MAPs from 130 to 1093 mm year^{-1} and that included desert shrubland, open shrubland, closed shrubland, grassland, savanna, evergreen needleleaf forest and mixed forest (Goulden *et al.*, 2012).

Gridded precipitation

We used the monthly precipitation estimates from the parameter-elevation regressions on independent slopes model (PRISM) for our analysis (Daly *et al.*, 2008). These data had a 2.5′ (*c.* 4 km) spatial resolution and extended from 1950 to 2010. PRISM is a knowledge-based climate analysis system that uses rain-gauge data from weather stations, a digital elevation model, additional spatial datasets and expert interaction to generate gridded precipitation estimates (Pinker *et al.*, 2003; Daly *et al.*, 2008). We refer to 'annual' as the integral of each hydrological year (September to August).

Land cover and land-cover change

We used land-cover information from the California Gap analysis project (CA-GAP) (Davis *et al.*, 1998) supplemented with the MODIS land-cover product (Friedl *et al.*, 2010) to examine the effect of plant structural type on interannual response to precipitation variation. The CA-GAP product was based on Landsat satellite imagery, aerial photography and field surveys. It provides distribution information on natural plant community types, land-use classes and widespread tree and shrub species. We cross-walked the CA-GAP vegetation types to the 17 IGBP land-cover types. Locations with vegetation cover of less than 10% were classified as barren. We used the MODIS IGBP land cover for locations where information on percentage life form (trees, shrubs, herbaceous) was not reported in the CA-GAP dataset.

Information on plant diversity was based on the presence of more than one dominant plant structural type. We grouped the pixels into six coarse plant structural categories, including those dominated by trees, woody shrubs, herbaceous plants and by mixtures of trees and shrubs, shrubs and herbaceous plants, and trees and shrubs. We also stratified tree and shrub pixels by leaf phenology (deciduous versus evergreen).

Wildfire is a natural part of California's ecosystem, which is often followed by rapid recovery of vegetation (Keeley *et al.*, 2006). We used a state-wide GIS layer of fire history since 1950 to infer the successional stage of vegetation at each location (http://frap.cdf.ca.gov/projects/fire_data/fire_perimeters/).

Responses of ecosystem function to variability in precipitation

Given sufficient time, ecosystems should adjust to the local climate and reach a new quasi-steady state. We therefore interpreted the spatial patterns of APAR across California as a measure of the long-term effect of climate on ecosystem structure and function, as mediated by gradual adjustments in population density, community composition, disturbance regime, soil properties and land-cover type. We averaged the annual precipitation and APAR during 2000–10 for each MODIS 1-km pixel, and during 1983–2006 for each GIMMS 8-km pixel, and fitted the long-term mean APAR against MAP across the entire state using a negative exponential curve. The spatial slope was then calculated as the derivative of the curve. Similarly, we capitalized on the large sample sizes generated by the remote sensing analysis and the wide precipitation ranges within each land-cover type to calculate a series of within-ecosystem-type spatial slopes.

We analysed how ecological function responded to comparatively rapid, interannual variation in precipitation. We performed robust linear regression of annual APAR against the simultaneous precipitation for each pixel. The slope of the regression is a measure of the sensitivity of vegetation production to year-to-year variation in precipitation, and the R^2 represents the fraction of variance explained by precipitation. The temporal sensitivity was then investigated as a function of climate (mean precipitation and precipitation variability), as well as ecosystem properties such as land-cover type and plant diversity. We quantified the overall interannual variability of precipitation and APAR for each pixel by the coefficient of variation (CV), which is the standard deviation divided by the long-term mean.

We further investigated how the temporal slope changes during recovery from fire for all pixels that burned during 1981 to 2005. The annual MODIS-derived APAR from 2001 to 2010 was used for the linear regression of APAR against precipitation for pixels that burned during 1981 to 2000. Only post-fire years of APAR were used for pixels that burned from 2001 to 2005. Areas that burned after 2005 were not analysed due to an inadequate number of post-fire years for a robust regression analysis. We summarized the temporal response for each 5-year age block within three of the dominant plant communities. Stand age was calculated as the time since most recent fire in 2006. The temporal slopes at locations that did not burn during 1980 to 2009 were calculated for comparison.

We performed a multiple linear stepwise regression to assess the relative importance of hydroclimate (MAP and natural variability in precipitation) and ecological factors (mean annual APAR and land-cover type) in controlling the temporal responses. Land cover was included as a categorical variable and all other variables were continuous. Two sets of stepwise regressions were performed, one for unburned areas and the other for areas that burned in 1980–2005. The latter included stand age as an explanatory variable.

The MODIS and GIMMS datasets produced very similar results (Fig. S1), implying that the 10-year record of MODIS data captured the variability over longer time periods. The MODIS observations offer higher spatial resolution than the GIMMs record, and our subsequent analysis therefore focuses on the MODIS-derived APARs, unless otherwise noted.

RESULTS

Spatial relationships between climate and mean APAR

The distribution of land cover (Fig. 1a) mirrors the hydrological climate (Fig. 1b), ranging from coniferous forest in the North Coast and Sierra Nevada regions with MAP more than 1000 mm year^{-1}, to barren or desert shrubland in the Mojave and Sonoran deserts with MAP less than 250 mm year^{-1}. Likewise, mean APAR (Fig. 1c,d) is closely correlated with climate, with high values in the North Coast and Sierra Nevada and low values in the south-eastern deserts. The Central Valley is dominated by intensively managed irrigated agriculture, resulting in patchy APAR values that are largely decoupled from MAP. The corresponding plant communities were arrayed along precipitation and APAR gradients (Table 1).

Mean annual APAR averaged over the 10-year MODIS record increased with increasing MAP before levelling off at a mean precipitation of 1000–1500 mm year^{-1} (Fig. 3a). We fitted an exponential curve of mean annual APAR (MJ m^{-2} year^{-1}) through the binned MAP (mm year^{-1}), yielding APAR = $2058.3(1 - e^{-0.0022\text{MAP}})$, with $R^2 = 0.98$ ($P < 0.001$). A similar relationship was found using the 24-year GIMMS-derived APAR data set (Fig. S1a). The slope of the spatial relationship was greatest in areas with low precipitation (Fig. 3c). We interpret the spatial relationship between MAP and APAR as a measure of

Table 1 Absorbed photosynthetically active radiation (APAR) and precipitation during 2001–10 summarized by land-cover type at 1-km resolution in California. Both mean and standard deviations are shown for the long-term mean annual precipitation (MAP, mm year^{-1}), Moderate Resolution Imaging Spectroradiometer (MODIS)-derived APAR (MJ m^{-2} year^{-1}), and their coefficients of variation (CV, dimensionless), temporal slope (MJ m^{-2} mm^{-1}) and R^2 of the linear regression of annual APAR (MJ m^{-2} year^{-1}) against precipitation (mm year^{-1}). Within-ecosystem spatial slope is also included.

	Number of pixels		Precipitation (mm year^{-1})		APAR (MJ m^{-2}yr^{-1})		Precipitation CV (%)		APAR CV (%)		Temporal slope (MJ m^2 mm^{-1})		R^2		Spatial slope (MJ m^2 mm^{-1})
Land cover	All	Unburned	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	
Evergreen needleleaf forest	70,710	62,971	1120	(460)	1810	(494)	27.8	(5.4)	6.4	(2.7)	0.03	(0.17)	0.14	(0.16)	0.42
Mixed forest	15,824	13,750	1271	(507)	1995	(370)	26.6	(4.8)	5.2	(2.2)	0.14	(0.19)	0.17	(0.19)	0.41
Closed shrublands	24,942	16,413	528	(256)	1560	(444)	42.3	(13.6)	7.9	(4.1)	0.33	(0.30)	0.36	(0.26)	1.04
Open shrublands	46,148	42,999	359	(303)	724	(461)	45.4	(16.7)	15.1	(8.6)	0.46	(0.53)	0.45	(0.26)	0.60
Woody savannas	35,731	32,487	724	(365)	1562	(433)	30.4	(7.0)	7.4	(3.3)	0.28	(0.37)	0.33	(0.25)	0.57
Savannas	22,004	19,990	566	(325)	1417	(496)	32.9	(10.8)	8.5	(4.5)	0.43	(0.45)	0.38	(0.26)	1.01
Grasslands	13,596	12,482	413	(210)	1188	(382)	35.7	(11.2)	11.8	(6.5)	0.70	(0.54)	0.47	(0.27)	1.14
Cropland	45,470	44,669	321	(185)	1447	(358)	37.4	(14.1)	10.9	(7.3)	0.38	(0.78)	0.23	(0.24)	0.91
Urban	10,467	9,704	409	(269)	1146	(466)	49.3	(18.6)	10.1	(7.0)	0.35	(0.34)	0.35	(0.25)	1.21
Desert shrubs	75,719	75,065	140	(75)	352	(166)	65.5	(10.9)	21.9	(7.7)	0.66	(0.35)	0.58	(0.19)	2.14
Barren	2771	2752	256	(285)	276	(248)	58.7	(17.7)	24.9	(14.4)	0.36	(0.47)	0.43	(0.26)	−0.01

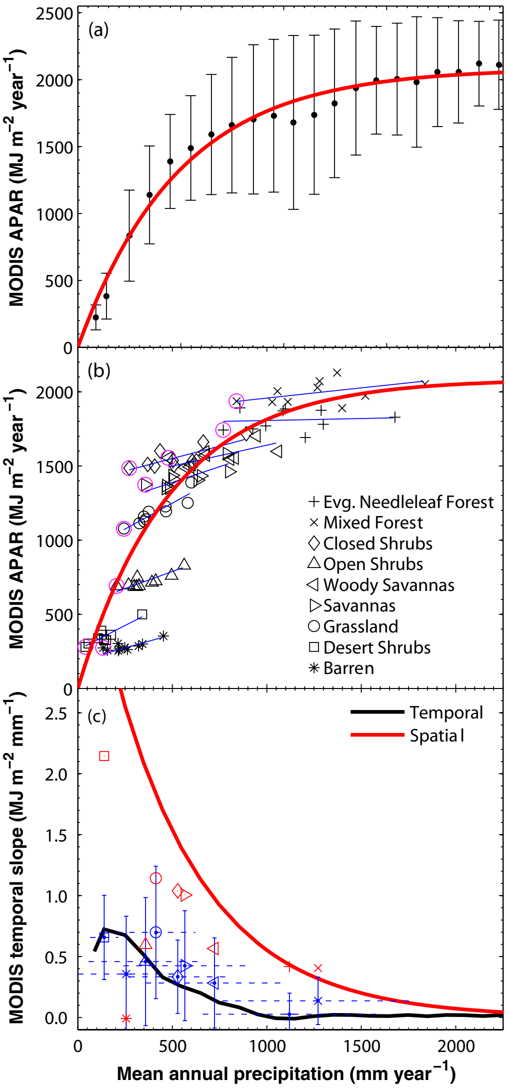

Figure 3 Annual Moderate Resolution Imaging Spectroradiometer (MODIS) absorbed photosynthetically active radiation (APAR; MJ m^{-2} year^{-1}) (a, b) and the slopes of the relationship between MODIS APAR and precipitation (MJ m^{-2} mm^{-1}) (c) as a function of mean annual precipitation (MAP; mm year^{-1}; 2001–10 mean) across California. APAR was averaged (a) during 2001–10 for MAP bins at 100 mm year^{-1} intervals, and (b) averaged within each year over each dominant land-cover type. The solid red lines in (a) and (b) show the overall fit between mean APAR and MAP across California, and in (c) the slope of the regression between mean APAR and MAP across the entire state (e.g. the derivative of the red line in a). The solid blue lines in (b) show the least squares regression for each land-cover type; the slopes of these lines provide a measure of the sensitivity of APAR to interannual precipitation variation within each cover type. The circled magenta symbols in (b) show the average APAR for each land-cover type during the driest observation year. In panel (c), the slope of the interannual APAR versus precipitation relationship was averaged across all pixels in 100 mm year^{-1} wide MAP bins (solid black line), and summarized for the dominant land covers (blue symbols and lines for mean and standard deviation); the red symbols represent the spatial slope within each land-cover type.

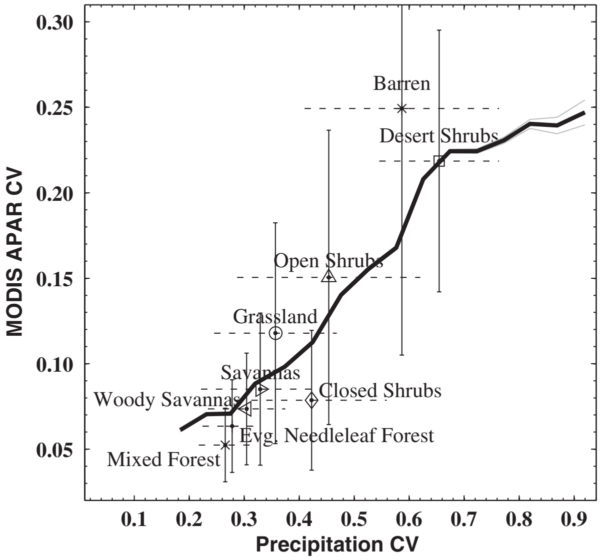

Figure 4 Interannual variability in Moderate Resolution Imaging Spectroradiometer (MODIS)-derived absorbed photosynthetically active radiation (APAR) during 2001–10 across California as a function of interannual precipitation variability. The coefficient of variation (CV; dimensionless) represents the normalized interannual variability. The thick black line shows the mean APAR CV for precipitation CV bins at 0.05 intervals. The thin lines show the 95% confidence intervals for the APAR CVs within the precipitation CV bins. The symbols show the average APAR and precipitation CVs for the dominant land-cover types, along with the corresponding standard deviations.

the long-term effect of climate on ecosystem function and structure, as mediated by gradual adjustments in population size and community composition.

Relationship between APAR and variability in precipitation

The interannual variability of satellite-derived APAR was positively related with variability in precipitation (Fig. 4). Forest experienced comparatively low interannual variability of precipitation, with a CV of less than 30% (Table 1, Fig. 4). Desert, barren and open shrubland experienced the greatest variability, with CVs of 66–45%. APAR variability was lowest in forested areas, with a CV of 5–7%, and greatest in desert and barren areas, with a CV of 22–25% (Fig. 4).

Effect of interannual precipitation variation on APAR

Relationship with climate

We calculated the response of APAR to variation in precipitation as interannual APAR deviation per unit of precipitation deviation in MJ m^{-2} mm^{-1} for each pixel and then averaged for each land-cover type (e.g. Fig. 3b,c). The slope of the interannual APAR versus precipitation relationship provides a measure of the short-term effect of weather on ecosystem function and structure, as mediated by rapid adjustments in plant physiology and leaf growth and senescence.

The interannual slope was greatest in drier areas, including the south-eastern desert and the grassland, shrubland and woodland ringing the Central Valley (Fig. S2a). The interannual slope was lowest in wetter regions, including evergreen and mixed forest along the north-west coast and in the Sierra Nevada, and forest and closed shrubland in southern California's mountains. The response was statistically insignificant over most forested areas, irrigated agriculture in the Central Valley and locations that burned during 2000 to 2010 (Fig. S2b–d).

The slope of the interannual response decreased with increasing mean precipitation before levelling off at a MAP of *c.* 1000 mm year^{-1} (Fig. 3c). Locations with a MAP of less than 300 mm year^{-1} had an average interannual slope of *c.* 0.5 MJ m^{-2} mm^{-1}; locations with a MAP greater than 1000 mm year^{-1} had an average interannual slope of less than 0.05 MJ m^{-2} mm^{-1}. Extremely dry locations, with a MAP of less than 100 mm year^{-1}, had an interannual slope that was somewhat below that of sites with a MAP of 200–300 mm year^{-1}.

The relationship between the temporal slope and the precipitation CV was peaked, reaching a maximum of 0.7 MJ m^{-2} mm^{-1} at a precipitation CV around 0.7, and decreasing at higher and lower precipitation CVs (Fig. 5a). Precipitation CV generally decreased with increasing MAP, and locations with the highest rainfall CVs were also among the driest on average.

The slope of the interannual response at a given mean precipitation was much lower than the spatial slope derived across the entire state, especially at MAPs below 1500 mm year^{-1} (Fig. 3b,c). The rapid response of APAR to interannual precipitation at 200 mm year^{-1} MAP was 0.7 MJ m^{-2} mm^{-1}, whereas the long-term APAR response to spatial variation in precipitation at this MAP was 2.9 MJ m^{-2} mm^{-1}. Similarly, the interannual APAR response at 1000 mm year^{-1} was less than 0.1 MJ m^{-2} mm^{-1}, whereas the long-term response of APAR at this MAP was 0.5 MJ m^{-2} mm^{-1}. The spatial slope derived from all pixels within a land-cover type (Fig. 3c, red symbols) was generally greater than the corresponding interannual slope, but less than the spatial slope across all land-cover types.

There was a strong linear relationship between annual precipitation and APAR across the landscape during the driest years ($r = 0.88$; Figure 3b); the robust linear fit through the APARs recorded for each vegetation type during the driest years increased by 1.95 MJ m^{-2} year^{-1} for each millimetre increase in MAP. This implies that the various plant communities have a similar maximum rain use efficiency, as reported by Huxman *et al.* (2004).

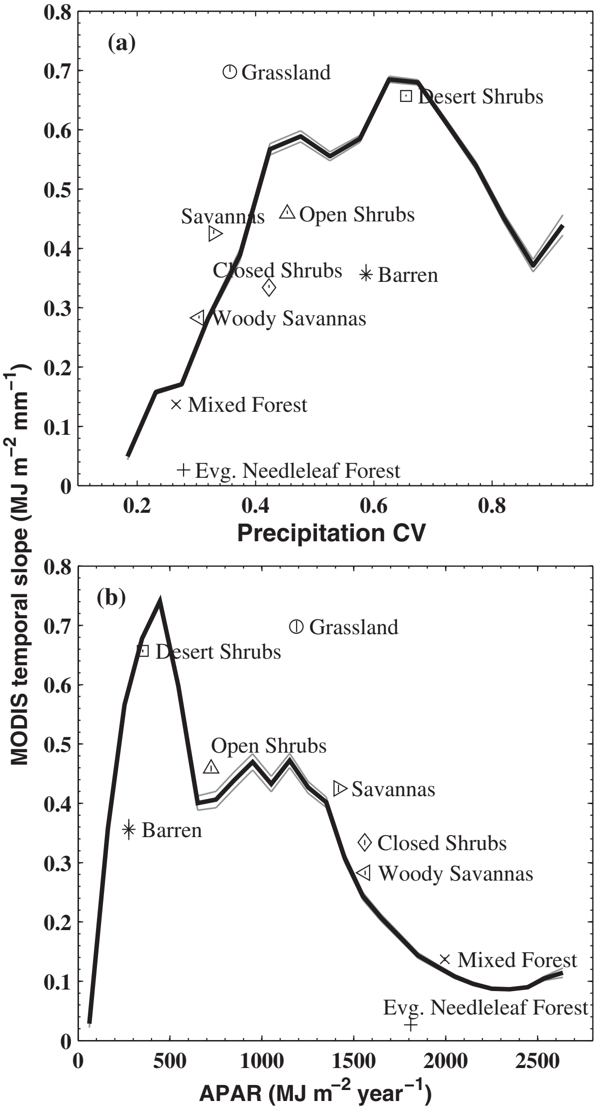

Figure 5 The slope of the interannual relationship between absorbed photosynthetically active radiation (APAR) and precipitation during 2001–10 (MJ m^{-2} mm^{-1}) as a function of (a) precipitation variability (Precipitation CV; dimensionless) and (b) mean APAR (MJ m^{-2} year^{-1}) during 2001–10. The thick black lines show the mean interannual slope in (a) 0.05-wide precipitation CV bins and (b) 100 MJ m^{-2} year^{-1} wide APAR bins, respectively, along with the corresponding 95% confidence shown by the thin lines. The symbols show the mean slope for the dominant land-cover types, along with the corresponding 95% slope confidence intervals in vertical lines.

Relationship with ecosystem properties

The temporal slope generally decreased across the gradient of mean APAR, from a maximum slope of 0.7 MJ m^{-2} mm^{-1} in areas with a mean APAR of 500 MJ m^{-2} year^{-1} to a slope of 0.1 MJ m^{-2} mm^{-1} in areas with a mean APAR of 2000 MJ m^{-2} year^{-1} (Fig. 5b). The temporal slope was similarly reduced at locations with very sparse vegetation and an APAR of less than 300 MJ m^{-2} year^{-1}. These sparsely vegetated sites also had a comparatively low MAP and high precipitation CV (Figs 3c & 5a).

Grasslands had the highest temporal slope among the land-cover types, with a mean of 0.70 MJ m^{-2} mm^{-1} (Fig. 5, Table 1). The high interannual slope observed for grassland was not

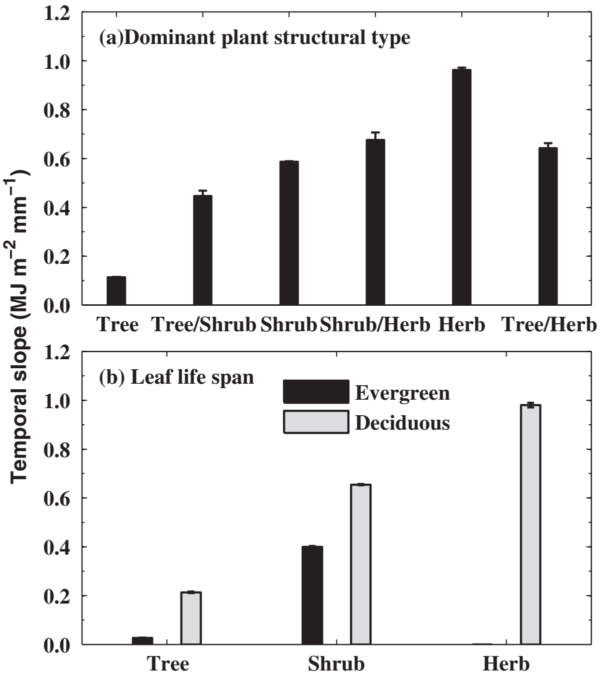

Figure 6 Effects of (a) the dominant plant structural type or types and (b) the dominant leaf life span on the slope of the interannual relationship between absorbed photosynthetically active radiation (APAR) and precipitation. 'Herb' indicates herbaceous vegetation such as grasses and forbs. The error bars show the 95% confidence intervals.

simply a consequence of the observed relationships between slope and MAP (Fig. 3c), precipitation CV (Fig. 5a) or mean APAR (Fig. 5b). Grassland had an anomalously high interannual slope compared with land-cover types such as savannas and shrublands that occupy broadly similar climates. Desert shrubland and open shrubland also responded strongly to interannual variation in precipitation, with temporal slopes ranging from 0.46 to 0.66 MJ m^{-2} mm^{-1}. Forest responded little, with slopes of less than 0.14 MJ m^{-2} mm^{-1} (Figs 3 & 5).

We grouped the pixels into six coarse plant structural categories, including those dominated by trees, shrubs, herbaceous plants and by mixtures of trees and shrubs, shrubs and herbaceous plants, and trees and shrubs. Locations dominated by herbaceous plants exhibited the greatest response of APAR to interannual variation in precipitation, whereas locations dominated by trees showed the lowest response and those dominated by shrubs showed an intermediate response (Fig. 6a). Locations with a mixture of structural types showed an intermediate sensitivity. Areas with both shrubs and grasses were less sensitive than those dominated by herbaceous plants alone, and more sensitive than those dominated by shrubs alone.

We also sorted locations by leaf phenology (Fig. 6b). Locations dominated by deciduous plants consistently exhibited a greater response of APAR to variation in precipitation. Deciduous shrubs (mostly coastal sage) had a temporal slope of 0.65–0.66 MJ m^{-2} mm^{-1} (95% confidence intervals [CI]), which was much higher than that of evergreen shrubs (e.g. chaparral) (0.39–0.40 MJ m^{-2} mm^{-1}). The majority of grassland in California is dominated by annual grasses and forbs, and these locations were highly sensitive to variation in precipitation.

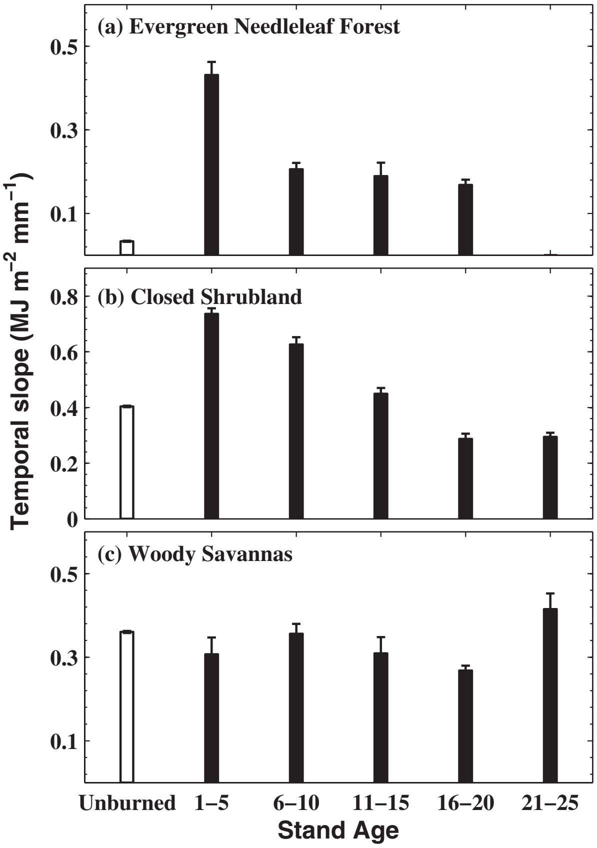

Figure 7 Effect of time since fire (stand age in years) on the slope of the interannual relationship between Moderate Resolution Imaging Spectroradiometer (MODIS) absorbed photosynthetically active radiation (APAR) and precipitation (MJ m^{-2} mm^{-1}) for (a) pixels classified as evergreen needleleaf forest, (b) closed shrubland including chaparral, and (c) woody savannas. The open bars in each panel show the mean interannual slope for locations with no reported fires since 1980. The slope of the interannual relationship between APAR and precipitation was calculated for 5-year periods following fire. Stand age was calculated as the number of years since fire in 2006. The error bars show the 95% confidence intervals.

Relationship with successional age following fire

Recently burned evergreen forest exhibited a much larger response of APAR to interannual variation in precipitation (95% CI, 0.40–0.46 MJ m^{-2} mm^{-1}) than did unburned forest (95% CI, 0.03–0.04 MJ m^{-2} mm^{-1}) (Fig. 7a). The response was greatest in the 5 years following fire and declined gradually with time but remained significant for at least 16 to 20 years after fire. Recently burned closed shrubland, which was mainly chaparral, also showed increased interannual sensitivity relative to unburned shrubland. The interannual slope for closed shrubland was at or below that observed for unburned shrubland within 11 to 15 years after fire (Fig. 7b), indicating that the decline in closed shrubland temporal slope was more rapid and complete than that observed for forest. No clear pattern was observed for savanna (Fig. 7c); the temporal slope of 1- to 5-year-old woody savanna (95% CI, 0.27–0.35 MJ m^{-2} mm^{-1}) was not significantly different from that of 6- to 10-year-old woody savanna (95% CI, 0.33–0.38 MJ m^{-2} mm^{-1}) and that of unburned woody savanna (0.36 MJ m^{-2} mm^{-1}).

Relative importance of controls on short-term APAR response

The effect of interannual variation in precipitation on APAR was significantly related to MAP, natural variability of precipitation, and mean annual APAR ($n = 241{,}272$, $P < 0.00001$ for all three factors; Table S2), and so we performed a multiple linear stepwise regression to assess the relative importance of these factors. The climatology of MAP was the most significant predictor for locations that had not burned since 1980, explaining 34% of the interannual slope variance (Table S2). Mean annual APAR, land-cover type and interannual variability of precipitation provided further significant explanatory variables, and the final repression explained 38% of the variance. We also performed a stepwise regression on pixels that burned after 1980, with stand age included as an explanatory variable. The precipitation climatology remained the most significant term, explaining 32% of variance. Precipitation variability, plant diversity, stand age and APAR were also significant, and the final regression explained 36% of the variance (data not shown). We note that MAP, precipitation CV and mean annual APAR were correlated with each other, with variance inflation factors ranging from 2.3 to 2.5. This moderate collinearity of the dependent variables creates a challenge for unambiguous attribution; the results of the stepwise regression should be interpreted with caution.

DISCUSSION

The APAR response peaks in areas with intermediate variability in precipitation and productivity

The APAR sensitivity to interannual precipitation peaked in areas with intermediate variability in precipitation, such as grassland and desert shrubland, and was muted in wet areas with dense forest vegetation and also in dry areas with very sparse vegetation (Figs 3 & 5; Knapp & Smith, 2001). The high interannual APAR sensitivity observed for most grassland and shrubland sites presumably reflects selection for plants that capitalize on episodic increases in precipitation, as would be expected given California's variable precipitation regime.

The reduced interannual APAR sensitivity at the driest sites, which also had particularly variable precipitation and very low mean APARs, probably reflects biotic constraints such as low meristem and seed densities that prevent the local vegetation from taking advantage of transient periods of increased moisture (Dalgleish & Hartnett, 2006). Production and APAR in forests may be limited by factors other than moisture, such as light, nitrogen availability or temperature, and an incremental change in precipitation has little effect on APAR (Huxman *et al.*, 2004). Our observations support the idea that interannual variability driven by precipitation peaks in areas of intermediate productivity where there is ample propagule availability and a lack of strong limitation on productivity by other factors such as light (Paruelo *et al.*, 1999; Knapp & Smith, 2001).

Other ecological controls on temporal response

Current climate, as measured by mean precipitation and precipitation variability, was not the only controller of APAR sensitivity to interannual precipitation. Interannual APAR sensitivity was influenced by fire and fire recovery, especially in closed shrublands and evergreen forest (Fig. 7). California's evergreen forest and closed shrubland are subject to severe crown fires that kill most of the aboveground vegetation (Keeley & Davis, 2007); woody savannas are subject to surface fires that mainly consume dry grasses and fine litter but often do not hurt the overstorey pines or oaks (Allen-Diaz *et al.*, 2007). Crown fires in evergreen forest and closed shrubland are followed by a succession from herbaceous plants to shrubs to trees, and a concomitant shift from deciduous to evergreen plants and an increase in growing season length (Keeley *et al.*, 2006). The increase in APAR sensitivity and subsequent recovery observed for evergreen forest and closed shrubland follows the trend expected based on plant succession following crown fire (Fig. 7). Recovery of savanna from a ground fire is much more rapid and does not involve shifts in dominant plant structural type, a pattern that is consistent with the constant interannual slope observed following fire.

APAR sensitivity to interannual precipitation was consistently higher for grassland than for shrubland or savanna, despite generally similar climates (Figs 3 & 5). The enhanced sensitivity for grassland appears to reflect the dominance of annual herbaceous vegetation in these communities, which allows very rapid changes in plant density and leaf area index with shifts in water input (M.L. Goulden *et al.*, in prep.). Ecosystems dominated by longer-lived plants, such as shrubs or trees, and by plants with evergreen foliage, were much less responsive to interannual variability in precipitation. Relatively more extractable water is available during drought for shrubs and trees with deeper roots, which may further decrease sensitivity to variation in precipitation (McIver *et al.*, 2009). Our temporal sensitivity may be underestimated for dense forests because NDVI, and thus the estimated APAR, may become less sensitive to changes in leaf area index over densely vegetated areas (Huete *et al.*, 2002).

Local plant diversity, as assessed by the presence of more than one dominant plant structural type, did not increase or decrease the temporal response. Rather, APAR sensitivity was a simple additive function of the sensitivities of the dominant plant types. For example, locations with a mix of shrubs and herbs had a sensitivity that was intermediate between those with just shrubs and those with just herbs. We did not find evidence that communities with a greater number of plant types are either more resistant (e.g., Tilman *et al*., 1996; Mulder *et al*., 2001) or less resistant to interannual variation in precipitation (Tilman *et al*., 1996; Pfisterer & Schmid, 2002; Reich *et al*., 2004; Hooper *et al*., 2005).

Relative APAR effects of short- versus long-term variation in precipitation

A comparison of two slopes, one from the within-site temporal relationship between interannual APAR and precipitation and the other from the across-site spatial relationship between mean APAR and MAP (both in units of MJ APAR m^{-2} per mm precipitation), provides a measure of the ecological impact of short-term fluctuations in precipitation relative to long-term climatic shifts (Walther *et al*., 2002; Kratz *et al*., 2003). The slope of the spatial relationship across the entire state was roughly five-fold greater than that of the interannual relationship at comparable MAP (Fig. 3c). Constraints such as plant structure, density and community composition apparently limit the response of APAR to interannual variation in precipitation. Long-term climate shifts that cause a shift in plant density and community type have an impact on ecosystem function that is much greater than that associated with short-term fluctuations in precipitation. The increased effect of long-term change in precipitation on APAR is presumably a result of gradual adjustments in population size and community composition that amplify the initial effect over time. This result mirrors previous reports (Sala *et al*., 1988, 2012; Lauenroth & Sala, 1992).

The within-ecosystem-type spatial relationship occupies an intermediate position between the interannual response and the between-ecosystem-type response. The slope of the within-ecosystem-type spatial relationship was roughly half that of the corresponding between-ecosystem-type spatial relationship, and two-fold greater than that of the corresponding temporal slope (Fig. 3c). This hierarchy of response mirrors that hypothesized by Smith *et al.* (2009). Hence, rapid changes in physiology and leaf area, which Smith *et al.* (2009) refer to as the ‘individual-level’ response, mediate the initial ecological effect of variation in precipitation. Slower changes in species-level population sizes and relative community composition, which Smith *et al.* (2009) referred to as ‘species reordering’, approximately double the magnitude of the initial response. Even slower changes in plant functional type and land cover classification, which Smith *et al.* (2009) referred to as the ‘species immigration’, lead to a second doubling of the response.

The spatial slope across the landscape was greatest for a MAP of 100–600 mm $year^{-1}$ (Fig. 5). This MAP range is apparently capable of supporting a wide diversity of ecosystem types, including open shrubland, grassland, savanna and closed shrubland (Table 1, Fig. 3c). The large spatial slope in this MAP range may be related in part to shifts in vegetation type, and corresponding changes in APAR. Hence, relatively modest shifts in precipitation in this range that ultimately result in a conversion from (for example) open shrubland to closed shrubland may cause a large change in APAR. In contrast, the spatial slope was comparatively low for MAP above 1000 mm $year^{-1}$. These areas were dominated by mixed and evergreen forest, which had similar and consistently high APARs.

Implications for predicting the ecological impact of climate change

Climate model runs for 2100 project a possible precipitation decrease in the south-western United States (e.g. Cayan *et al*., 2010). Our comparison of the temporal and spatial relationships between precipitation and APAR indicates that the impact of changing precipitation in California will depend strongly on temporal scale. A 100 mm $year^{-1}$ decrease in precipitation (20%) from an original MAP of 500 mm $year^{-1}$ would be expected to decrease APAR by 25 MJ m^{-2} $year^{-1}$ (*c.* 2%) in the first year (Fig. 3c) and 170 MJ m^{-2} $year^{-1}$ (*c.* 12%) once the vegetation has fully adjusted to the new MAP (Figs 3a & S3). This analysis assumes that precipitation alone controls APAR; temperature and other factors that may covary with MAP are disregarded. Nonetheless, the analysis illustrates the importance of determining whether re-equilibration occurs in a matter of decades or whether hundreds or thousands of years are required. Predictions of the year 2100 impact of a precipitation decline from a MAP of 500 mm $year^{-1}$ differ six-fold depending on whether equilibration takes a few decades or several centuries.

Most ecological investigations are made at local, short timescales (less than one to three decades; Walther *et al*., 2002). Experimental studies on the ecological effects of climate change have often relied on short-duration manipulations (Schwilk *et al*., 2009). Many of these studies may have probed the ecological effects of short-term meteorological variation rather than long-term climate change, with implications for the magnitude of response and the extrapolation to future conditions. Ecosystems should ultimately adjust to climate change through shifts in population density and community composition, but many observational and experimental studies are too brief to allow these processes to occur. Uncertainty over the rate at which ecosystems will respond to climate change, and the time required for adjustment, impose a major constraint on our ability to forecast the impact of climate change (Kratz *et al*., 2003; Guisan & Thuiller, 2005; Neilson *et al*., 2005).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Figure S1 Results from GIMMS (1983–2006) dataset.
Figure S2 Spatial distributions.
Figure S3 Prediction.
Table S1 Flux tower sites.
Table S2 Stepwise linear regression results.

BIOSKETCHES

Yufang Jin is a research scientist at the University of California, Irvine. Her research interests focus on large-scale monitoring of ecosystem dynamics and the associated drivers and consequences for climate. She uses primarily satellite remote sensing observations and geospatial techniques, in combination with field measurements and biogeochemical modelling, to investigate the processes and feedbacks in the complex climate–vegetation–human system.

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