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Photosynthetic activity of US biomes: responses to the spatial variability and seasonality of precipitation and temperature

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Abstract

We examined the response of the normalized difference vegetation index, integrated over the growing season (gNDVI) to mean precipitation, maximum temperature ($T_{\max}$), and minimum temperature ($T_{\min}$) over an 11-year period (1990–2000) for six biomes in the conterminous United States. We focused on within- and across-biome variance in long-term average gNDVI, emphasizing the degree to which this variance is explained by spatial gradients in long-term average seasonal climate. Since direct measurements of ecosystem function are unavailable at the spatial and temporal scales studied, we used the satellite-based gNDVI as a proxy for net photosynthetic activity.

Forested and nonforested biomes differed sharply in their response to spatial gradients in temperature and precipitation. Gradients in mean spring and fall precipitation totals explained much of the variance in mean annual gNDVI within arid biomes. For forested biomes, mean annual gNDVI was positively associated with mean annual and seasonal $T_{\min}$ and $T_{\max}$. These trends highlight the importance of the seasonal components of precipitation and temperature regimes in controlling productivity, and reflect the influence of these climatic components on water balance and growing-season length. According to the International Panel on Climate Change (IPCC) (2001) increases in temperature minima and fall precipitation have contributed the dominant components of US increases in temperature and precipitation, respectively. Within the range of conditions observed over the study region, our results suggest that these trends have particularly significant consequences for above-ground plant productivity, especially for Grassland, Open Shrubland, and Evergreen Needleleaf Forest. If historical climatic trends and the biotic responses suggested in this analysis continue to hold, we can anticipate further increases in productivity for both forested and nonforested ecoregions in the conterminous US, with associated implications for carbon budgets and woody proliferation.

Keywords: biome, climate, plant-productivity, remote sensing, seasonality, United States

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Introduction

There is strong evidence of directional trends in temperature and precipitation at regional and global scales (IPCC, 1996, 2001; Hulme & Viner, 1998). Moreover, changes in temperature and precipitation dynamics, largely through their control over water balance and growing-season length, have been identified as probable drivers of change in terrestrial productivity (Woodward, 1987; Myneni *et al.*, 1997; Wang *et al.*, 2001; Nemani *et al.*, 2002) and in the distribution of vegetation functional types (Neilson, 1986; Brown *et al.*, 1997; Allen & Breshears, 1998). Thus, regional- to global-scale changes in climate patterns could have substantial consequences for terrestrial productivity and carbon dynamics (IPCC, 1996; Jackson *et al.*, 2002).

Spatial variation in productivity, both within and across biomes, derives from gradients in moisture, temperature, and energy that occur within or cross over limits defining the suitability range for given biomes. Given that such climatic limits interact seasonally, and are often keyed to certain phenological stages, we can

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expect that the seasonality of climate changes will play a significant role in determining ecosystem response (Neilson, 1986; White *et al.*, 2000; Nemani *et al.*, 2002) and these responses will differ by biome type (VEMAP Members, 1995; Kramer *et al.*, 2000).

Large-scale, empirical studies of vegetation/climate coupling have often concentrated on associations between productivity and climate through time, either at specific locations, or averaged over regions (e.g. Le Houerou *et al.*, 1988; Sala *et al.*, 1988; Goward & Prince, 1995; Myneni *et al.*, 1997; Los *et al.*, 2001). For example, positive associations have been found between year-to-year changes in precipitation and both NDVI (Paruelo & Lauenroth, 1998; Kawabata *et al.*, 2001) and ANPP (Le Houerou *et al.*, 1988) in arid and semi-arid ecosystems.

The seasonality of precipitation, an important determinant of soil-water budgets (Dingman, 1994) has also been shown to influence productivity through interaction with the physiology, physiognomy, or life history of different vegetation types (Stephenson, 1990; Shinoda, 1995; Richard & Poccard, 1998; Kramer *et al.*, 2000). For example, Epstein *et al.* (1999) reported that field-measured ANPP is related to the seasonality of precipitation for shrublands and grasslands. This finding is consistent with other work illustrating the role of the annual course of water-balance in structuring the geographic distribution of major vegetation formations (Walter, 1971; Neilson *et al.*, 1992; Prentice *et al.*, 1992; Paruelo & Lauenroth, 1996).

Studies on NDVI–temperature relationships (Braswell *et al.*, 1997; Yang *et al.*, 1997, 1998; Potter & Brooks, 1998) have emphasized the importance of growing-season length in controlling annual productivity. However, there is little large-scale empirical work on the differential responses of vegetation activity to maximum temperature, minimum temperature, or seasonal maxima and minima for different biomes (Alward *et al.*, 1999). Potter & Brooks (1998) and Wang *et al.* (2001) both examined the response of NDVI to maximum and minimum temperatures, but restricted their analyses to intra-annual time scales. Alward *et al.* (1999) reported that productivity in some grassland types is more responsive to elevated minimum temperatures, but did not consider other biome types.

In this study, we used satellite and climate data to assess the degree to which spatial gradients in productivity are driven by gradients in long-term average climate characteristics, both within and across major biomes (e.g. Lauenroth & Sala, 1992; Paruelo *et al.*, 1999). Specifically, we examined spatial associations between average annual photosynthetic activity and long-term averages of annual and seasonal precipitation, temperature minima ($T_{\min}$), and temperature maxima ($T_{\max}$) within the period 1990–2000 for the conterminous US. The normalized difference vegetation index, integrated over the growing season (gNDVI) was used as a proxy for annual photosynthetic activity due to its consistent availability over broad spatial and temporal scales (Asrar *et al.*, 1984; Sellers *et al.*, 1992; Myneni *et al.*, 1997). Our primary goal was to evaluate the relative contribution of seasonal climate characteristics in governing spatial gradients in productivity within and across biomes.

Materials and methods

NDVI data

We acquired AVHRR data for the conterminous US from the USGS EROS Data Center. This data set contains biweekly composited NDVI images at approximately 1 km spatial resolution (Eidenshink, 1992). The data are georeferenced to the Lambert Azimuthal Equal-Area map projection. We produced monthly NDVI composites for January 1990–December 2000 by selecting the maximum NDVI value for each successive pair of biweekly composites. Monthly maximum value compositing further reduces atmospheric and sensor scan angle effects on NDVI (Spanner *et al.*, 1990; Moody & Strahler, 1994).

NDVI is based on the contrast between red (R) and near-infrared (NIR) reflectance of solar irradiance by vegetation (Holben, 1986):

$$\mathrm{NDVI} = (\mathrm{NIR} - \mathrm{R})/(\mathrm{NIR} + \mathrm{R}). \qquad (1)$$

The R and NIR detectors on the AVHRR sensors record radiance in the 0.58–0.68 μm and 0.725–1.1 μm wavelength regions, respectively. NDVI varies theoretically between −1.0 and +1.0 (Holben, 1986), and increases from about 0.1 to 0.75 for progressively increasing amounts of vegetation (Myneni *et al.*, 2001). The NDVI is most directly related to the fraction of photosynthetically active radiation (fPAR) absorbed by vegetation canopies (Asrar *et al.*, 1984; Choudhury, 1987), and hence to photosynthetic activity of terrestrial vegetation (Sellers *et al.*, 1992; Myneni *et al.*, 1995).

Although NDVI only approximates terrestrial vegetation activity, and despite sources of variance related to atmospheric conditions, calibration discrepancies, and variability in illumination/view geometry (Moody & Strahler, 1994) AVHRR data currently provide our best empirical device for approximating spatio-temporal variability in terrestrial plant productivity at large scales.

Temperature and precipitation data

For the period 1990–2000, we obtained monthly precipitation totals and monthly averages of mean, minimum, and maximum temperature from the US Historical Climatology Network (USHCN) for 249 meteorological stations distributed throughout the conterminous US (Karl *et al.*, 1990) (Fig. 1). These data are subject to quality control assessment and adjustment procedures described by Karl *et al.* (1990).

Land-cover map

We used the 1 km land-cover map of North America from the USGS-NASA Distributed Active Archive Center. This map is derived from 1 km AVHRR data spanning April 1992–March 1993 (Loveland *et al.*, 1999). In this study, we adopted the International Geosphere–Biosphere Programme (IGBP) land-cover taxonomy, from which 17 classes are identified within the conterminous US (Loveland *et al.*, 1999).

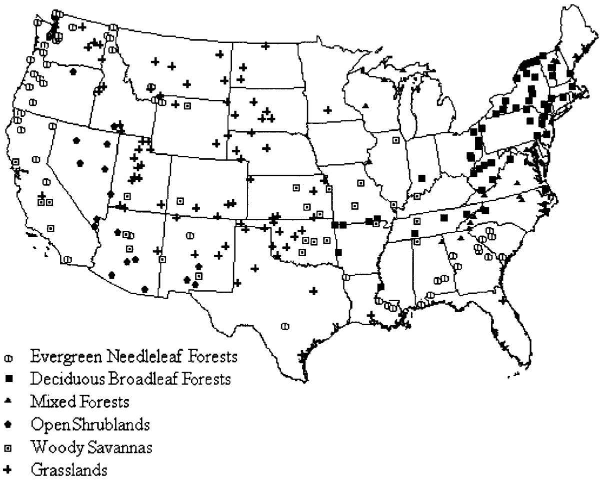

Fig. 1 Distribution of the 249 meteorological station locations used in this study, and the dominant biome type at each station.

Analysis

The climate data, land-cover data and monthly NDVI composites were all georeferenced to the Lambert Azimuthal Equal-Area projection and co-located. Thus, for the single pixel containing each climate station, we extracted land-cover type, monthly NDVI, and monthly climate data for the 11-year study period. Six IGBP vegetation types were represented among the 249 stations (Table 1, Fig. 1). We used a single AVHRR pixel for each station in order to avoid smoothing out the variability in the NDVI data. Of the 249 climate stations used, 93% had the same land-cover class as the majority of surrounding pixels within a 3×3 window.

We calculated the growing-season NDVI totals (gNDVI) to approximate the annual photosynthetic activity of vegetation at each station (Asrar *et al.*, 1984; Myneni *et al.*, 1995). We defined the growing season as the period during which monthly NDVI values were greater than or equal to 0.1, after Myneni *et al.* (2001). Annual and seasonal precipitation totals, and annual and seasonal averages of mean-monthly $T_{\max}$ and $T_{\min}$ were calculated from the climate records at each station. All variables were averaged over the 11-year study period so that we could examine the relationships between gradients in long-term means of gNDVI and climate.

We used the coefficient of variation (CV) to characterize interannual variability in gNDVI and each climate variable at each station. The CV provides a standardized temporal variance of a given variable (x) at a particular location (i) relative to the long-term mean at that location ($\bar{x}_i$):

$$\mathrm{CV}x_i = \sigma_{x_i}/\bar{x}_i \times 100\%, \tag{2}$$

where σ_{x_i} is the standard deviation of variable x at i. The CV values for each variable were used to examine whether temporal variability in gNDVI and temporal

Table 1 The biome types identified for the 249 meteorological stations and the number of stations for each biome

IGBP class	Biome type	Number of stations	Definition (Belward & Loveland, 1996)
1	ENF	50 (28)	Canopy cover >60% and height >2 m. Most of the canopy remains green all year
4	DBF	55 (32)	Canopy cover >60% and height >2 m. Most of the canopy is deciduous
5	MF	22 (6)	Canopy cover >60% and height >2 m. Mixed evergreen and deciduous canopy
7	OSH	17 (11)	Woody vegetation cover between 10% and 60%, >2 m. Evergreen or deciduous canopy
8	WS	27 (7)	Canopy cover between 30% and 60%, and height >2 m. Deciduous or evergreen canopy. Herbaceous or other understory vegetation
10	Gr	78 (42)	Herbaceous cover. Woody cover <10%
Total		249 (126)	

The number of stations for which the class labels from the AVHRR and MODIS land-cover maps agreed are given in parentheses. ENF, Evergreen Needleleaf Forest; DBF, Deciduous Broadleaf Forest; MF, Mixed Forest; OSH, Open Shrubland; WS, Woody Savanna; Gr, Grassland.

variability in climate were related across stations. The CV has been used extensively as an index of variability for both climatic and ecological data (Le Houerou *et al.*, 1988; Lauenroth & Sala, 1992; Frank & Inouye, 1994) and has been demonstrated to reflect the differential capacity of different ecosystems to buffer interannual climatic variations (Paruelo & Lauenroth, 1998).

For within-biome analysis, we examined gNDVI–climate associations across all the individual stations within each biome, thus treating within-biome observations as independent samples. Linear and nonlinear regression models were developed using gNDVI and climate data for the stations within each biome (Fig. 1, Table 1). For across-biome analysis, we averaged the values of gNDVI and climate over all of the individual stations for each biome, thus treating each biome as independent from the others, and ignoring within-biome variability. We used linear regression and correlation analysis to examine relationships between biome-level means of gNDVI and climate variables. Given the substantial distances between them, we assumed spatial independence of the stations, both within and across biomes.

Results

Within-biome relationships between gNDVI and climate

Long-term means of gNDVI and precipitation. Within each biome, 11-year mean annual gNDVI was positively associated with mean annual precipitation (MAP) (Table 2, Fig. 2). The strength of this relationship varied across biomes. For example, Mixed Forest and Woody Savanna produced much stronger r^2 values than Deciduous Broadleaf Forest or Grassland (Table 2).

Table 2 R^2 and P-values of relationships between 11-year mean of gNDVI and means of annual and seasonal precipitation (MAP) within each biome

IGBP class	MAP	Spring	Summer	Fall	Winter
ENF	**0.42**	**0.35**	0.16	**0.20**	0.14
	<**0.001**	<**0.001**	0.004	**0.001**	0.006
DBF	**0.25**	**0.36**	0.00	0.03	**0.26**
	<**0.001**	<**0.001**	>0.10	>0.01	<**0.001**
MF	**0.59**	**0.59**	0.15	0.14	**0.54**
	<**0.001**	<**0.001**	0.07	0.09	<**0.001**
OSH	**0.41**	**0.28**	0.02	0.36	0.15
	0.006	**0.029**	>0.10	0.10	>0.10
WS	**0.62**	**0.65**	**0.28**	**0.57**	0.15
	<**0.001**	<**0.001**	**0.005**	<**0.001**	0.048
Gr	**0.28**	**0.42**	0.11	**0.25**	0.10
	<**0.001**	<**0.001**	0.003	<**0.001**	0.004

Cells with $R^2 \geq 0.2$ and significant at $P \leq 0.05$ are shown in bold.

ENF, Evergreen Needleleaf Forest; DBF, Deciduous Broadleaf Forest; MF, Mixed Forest; OSH, Open Shrubland; WS, Woody Savanna; Gr, Grassland.

Associations between 11-year means of gNDVI and seasonal precipitation also varied by biome, as well as by season (Table 2). For all vegetation types except Open Shrubland, gNDVI was more strongly related to spring precipitation than to precipitation for any other season. This was especially notable for Deciduous Broadleaf Forest, Grassland, and Woody Savanna (Fig. 3). In general, gNDVI was also associated with fall precipitation, except for Deciduous Broadleaf Forest and Mixed Forest, which were the only two biomes to exhibit strong associations between gNDVI and winter precipitation (Table 2). Overall, the weakest seasonal relationships were between gNDVI and summer precipitation (Table 2).

We identified two statistical groupings of Grassland stations (Fig. 2f) and reanalyzed these subgroups separately (Fig. 4a). The association between gNDVI and precipitation was much stronger for the less productive subgroup ($r^2 = 0.53$, $P < 0.0001$) than for the more productive subgroup ($r^2 = 0.20$; $P < 0.003$). In both cases, gNDVI was most closely associated with spring precipitation (less productive group: $r^2 = 0.42$, $P < 0.0001$; more productive group: $r^2 = 0.35$, $P < 0.0001$).

We compared the geographic distribution of the two subgroups within the Grassland class (Fig. 4a) with published distributions of grassland functional type (Paruelo & Lauenroth, 1996; Still *et al.*, 2003) and morpohological and compositional characteristics (Ricketts *et al.*, 1999). Based on these comparisons, the less productive subgroup appearing in the data (Figs 2f and 4a) exhibited closest spatial correspondence to northern and northwestern mixed grasslands, western short grasslands, palouse grasslands, and grassland/shrubland transition zones on the Colorado Plateau (Ricketts *et al.*, 1999). The more productive subgroup generally corresponded to central and southern mixed grasslands, and grasslands transitioning to forest, particularly in the central forest/grassland transition zone through Oklahoma, shrub steppe/montane forest transitions around the periphery of the Great Basin in Utah and Idaho, and montane valley and foothill grasslands in western Montana.

A closer investigation of Mixed Forest also revealed two distinct groups that are fundamentally different in their productivity and climatic characteristics. One group, characterized by higher gNDVI and higher MAP (Fig. 2c) is restricted to the Appalachian/Blue Ridge province in the southeastern US (Fig. 4b) with a few stations on the mid-Atlantic piedmont. The other group is mostly restricted to the northeastern hardwood/boreal transition. Taken separately, gNDVI

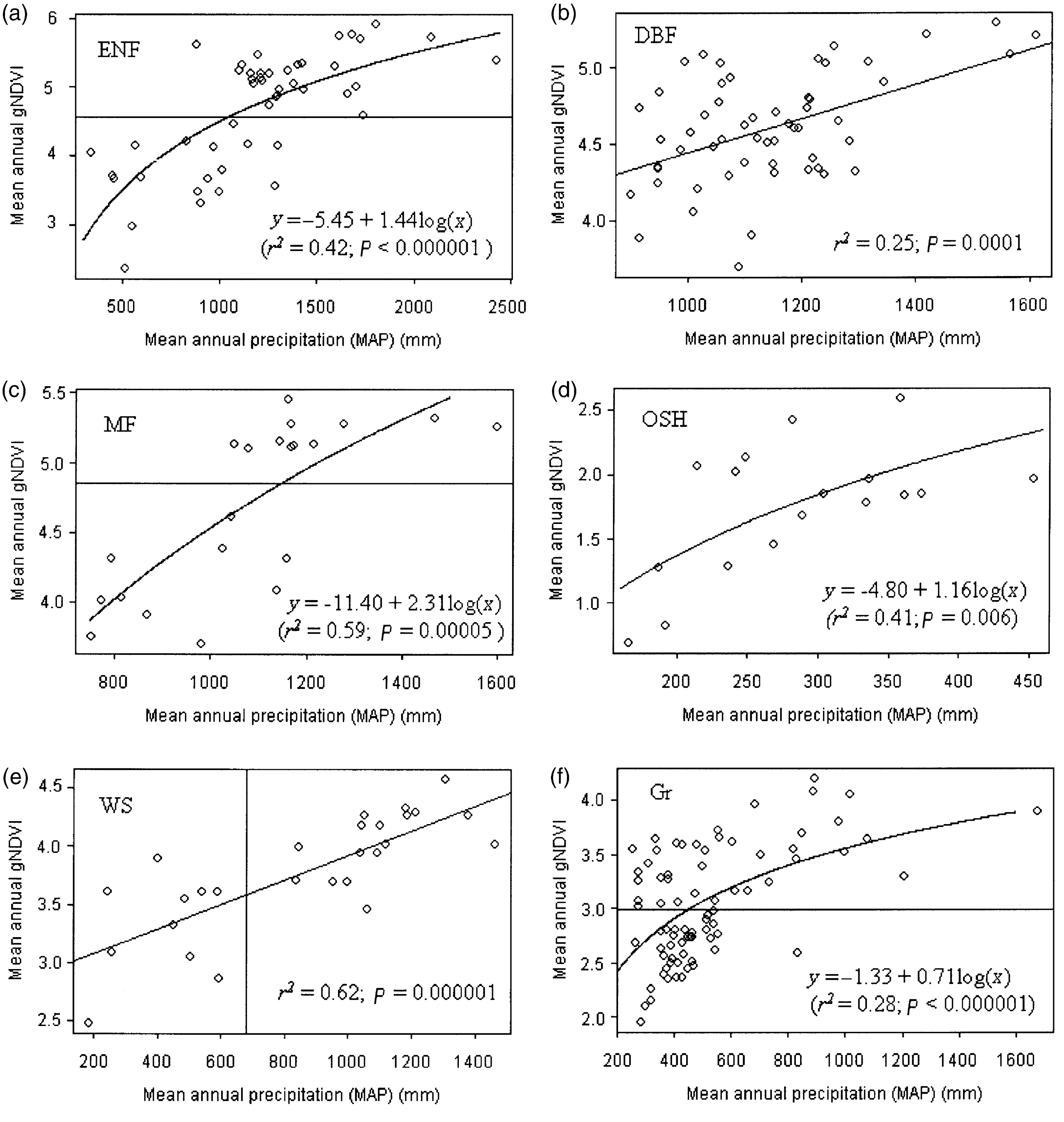

Fig. 2 Relationships between 11-year means of gNDVI and annual precipitation for each biome: (a) Evergreen Needleleaf Forest (ENF); (b) Deciduous Broadleaf Forest (DBF); (c) Mixed Forest (MF); (d) Open Shrubland (OSH); (e) Woody Savanna (WS); (f) Grassland (Gr). Horizontal lines in (a), (c), and (f), and the vertical line in (e) represent divisions between subgroups within these biomes. These subgroups are mapped in Fig. 4.

for these two groups was not significantly associated with MAP or any seasonal precipitation variables.

As with Mixed Forest, gNDVI/precipitation relationships for Evergreen Needleleaf Forest and Woody Savanna were also driven by two subgroups within their respective biomes (Fig. 2a and e). The most productive and wettest Evergreen Needleleaf Forest stations were restricted to the US southeast, and the coastal margin of the Pacific Northwest. The less productive stations were mostly located in the interior of the Pacific Northwest (Figs 2a and 4c). The wetter, more productive Woody Savanna stations were distributed through the lower Great Plains and upper Mississippi Valley, and the drier, less productive stat-

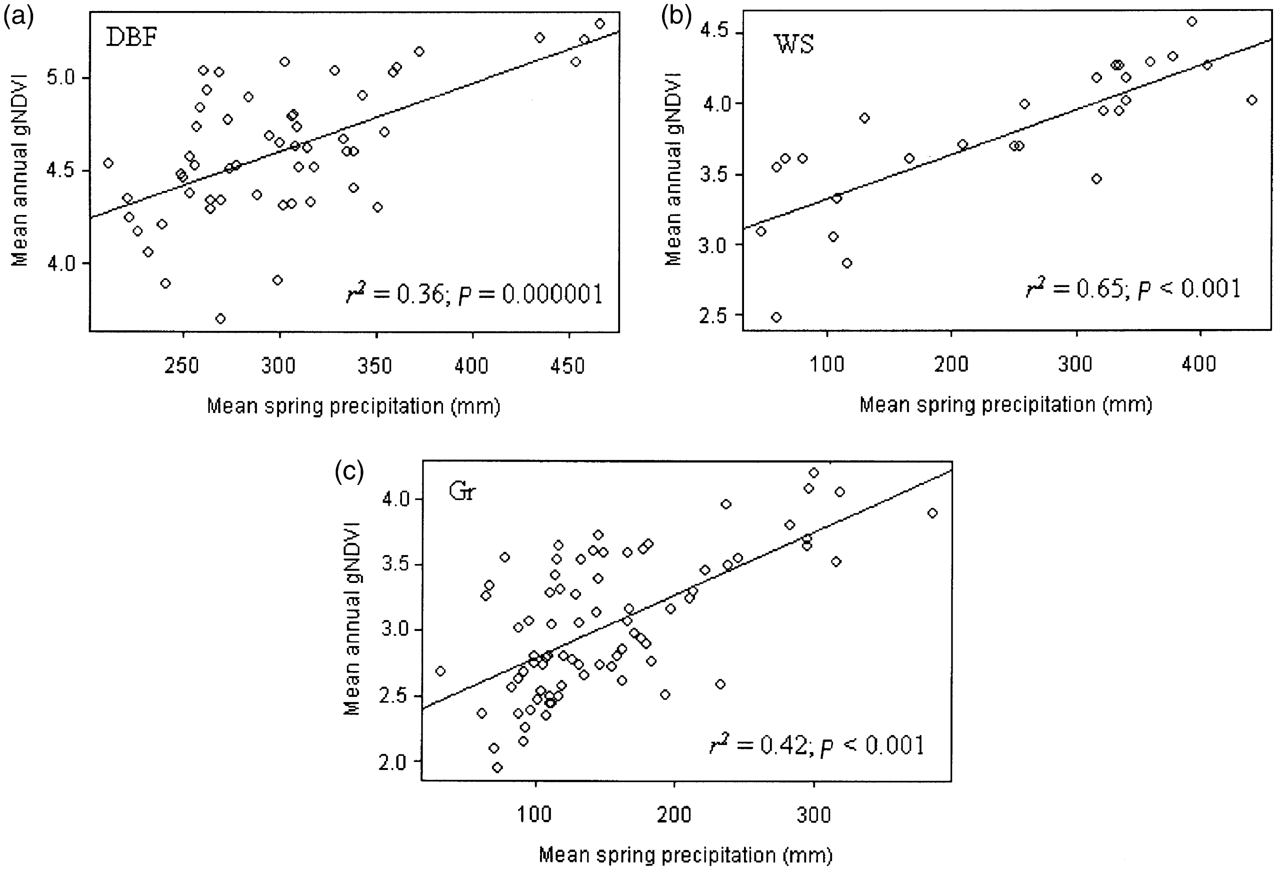

Fig. 3 Relationships between 11-year means of gNDVI and spring precipitation for three biomes: (a) Deciduous Broadleaf Forest (DBF); (b) Woody Savanna (WS); (c) Grassland (Gr).

ions were scattered about the US southwest (Figs 2e and 4d).

Interannual variability in gNDVI and precipitation. Open Shrubland exhibited a significant (positive) relationship between the CV of gNDVI and CV of annual precipitation ($r^2 = 0.26$, $P = 0.037$) and summer precipitation ($r^2 = 0.56$, $P = 0.0006$). For Grassland, the CV values of gNDVI and fall precipitation were also positively correlated ($r^2 = 0.36$, $P < 0.0001$).

Long-term means of gNDVI, T_{min}, *and* T_{max}. For the three forest biomes, gNDVI had significant positive associations with all long-term averages (annual and seasonal) of both $T_{\min}$ and $T_{\max}$ (Table 3, Figs 5a–c and 6a–c). In comparison, gNDVI for the most arid biomes, Open Shrubland and Grassland, was not associated with any temperature variable. Woody Savanna produced weak-to-moderate associations with $T_{\min}$ for spring, summer, and fall (Table 3). For Evergreen Needleleaf Forest, gNDVI was more strongly associated with $T_{\min}$ than $T_{\max}$, and was most strongly associated with winter, followed by spring and fall temperatures. As with annual precipitation, these results may actually reflect relationships across subgroups within Woody Savanna and Evergreen Needleleaf Forest, and most certainly for Mixed Forest.

Interannual variability in gNDVI, T_{min}, *and* T_{max}. Overall, CV of gNDVI for Mixed Forest and Woody Savanna were more strongly associated (positive) with CV of temperature means than other biomes (Table 4). These associations for Mixed Forest were significant for the CV of annual, winter, and spring temperature means for both $T_{\max}$ and $T_{\min}$. In contrast, CV of gNDVI for Woody Savanna was associated with CV of annual, summer, and fall $T_{\min}$ (and only spring $T_{\max}$).

Across-biome relationships between gNDVI and climate

Mean annual gNDVI was greatest for the three forest biomes (4.61–4.72), intermediate for Woody Savanna and Grassland (3.77 and 3.04, respectively) and low for Open Shrubland (1.75) (Table 5). Likewise, MAP was high and roughly equal for the forest biomes (1142–1269 mm yr^{-1}), intermediate for Woody Savanna

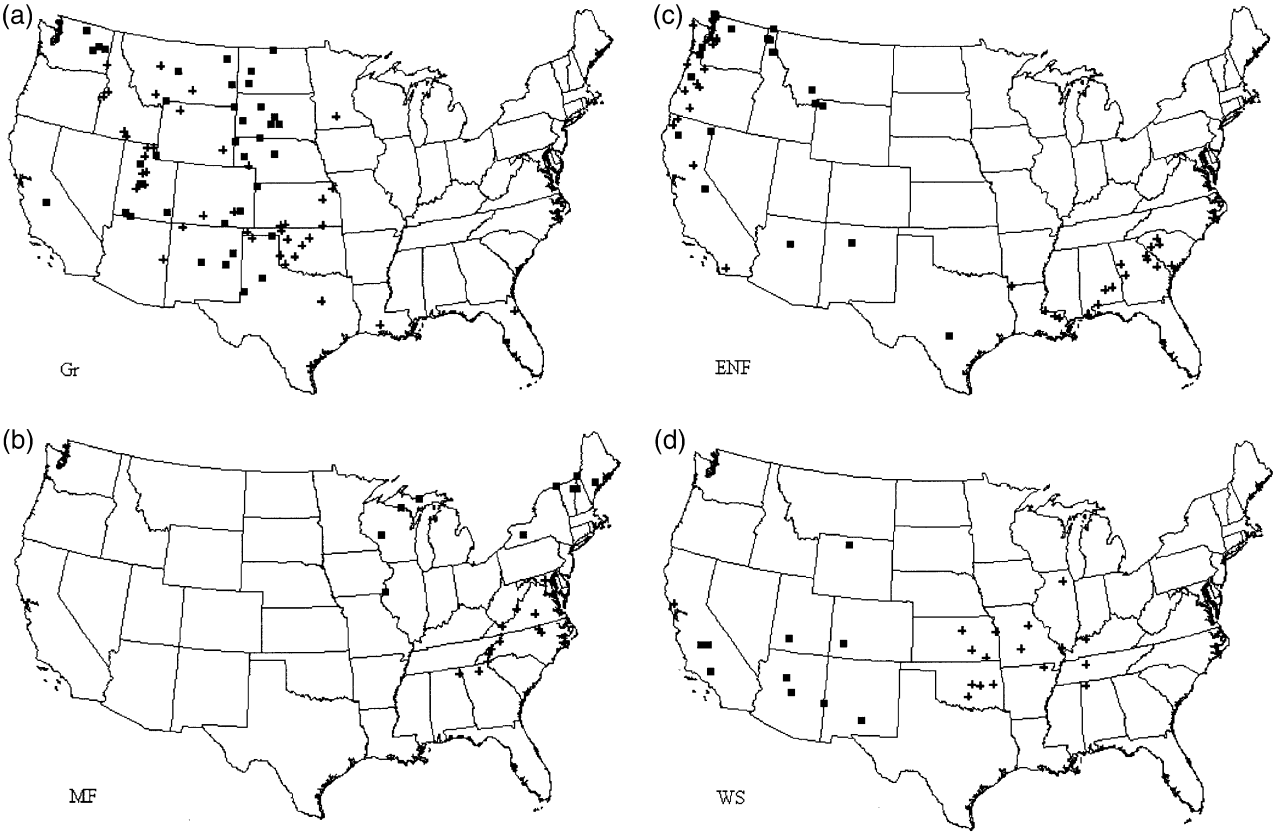

Fig. 4 Spatial distributions of the within-biome subgroups identified in Fig. 2: (a) Grassland (Gr); (b) Mixed Forest (MF); (c) Evergreen Needleleaf Forest (ENF); (d) Woody Savanna (WS). In each case, square symbols represent the less productive subgroup and cross symbols represent the more productive subgroup as seen in Fig. 2.

and Grassland (857 and 523 mm yr^{-1}, respectively) and low for Open Shrubland (285 mm yr^{-1}). Mean annual gNDVI was, thus, strongly correlated with MAP across the six biomes (Fig. 7a), as well as with mean precipitation for each season, especially spring and fall (Fig. 7b and d).

The mean CV of gNDVI was similar across biomes, ranging from roughly 10.0% for the forest biomes, to 13.4% for Grassland. The exception was Open Shrubland, with a mean CV of 28.04%. Open Shrubland also exhibited substantially higher interannual variability in MAP and in precipitation for each season.

Across biomes, mean CV of gNDVI was significantly associated with mean CV of annual and seasonal precipitation totals. However, these relationships were driven by Open Shrubland. When this class was removed there were no significant relationships between interannual variability of gNDVI and precipitation.

The three forest biomes had the lowest mean T_{max} values for both summer and winter, except for Evergreen Needleleaf Forest, which had a high mean winter T_{max} due to the effect of averaging values from southeast and northwest conifer forests. The three nonforest biomes had relatively high T_{max}, and Open Shrubland was always the highest. Evergreen Needleleaf Forest had the highest mean winter T_{min}, followed by Open Shrubland and Woody Savanna. The other three biomes had relatively low winter T_{min} (Table 5).

Across biomes, mean annual gNDVI was negatively correlated with mean summer T_{max} (Fig. 8). Mean annual gNDVI was not related to any other T_{max} variable, or to mean annual or seasonal T_{min} values. The CV values of gNDVI were not significantly associated with CV of annual or seasonal means of T_{max} or T_{min}. A significant relationship between mean CV of gNDVI and CV of summer average T_{min} ($r^2 = 0.65$, $P < 0.02$) was heavily influenced by Open Shrubland, which exhibited high interannual variability in both gNDVI and average summer T_{min}.

Discussion

Within-biome relationships between gNDVI and climate

Long-term means of gNDVI and precipitation. Strong association between gNDVI and MAP observed for all

Table 3 R^2 and P-values of relationships between 11-year mean annual gNDVI and means of annual and seasonal averages of $T_{\max}$ and $T_{\min}$ within each biome

IGBP class	Annual	Spring	Summer	Fall	Winter
ENF	0.17	**0.29**	0.11	**0.29**	**0.41**
	0.003	***<0.001***	*0.02*	***<0.001***	***<0.001***
	0.41	**0.39**	**0.25**	**0.41**	**0.51**
	<0.001	***<0.001***	***<0.001***	***<0.001***	***<0.001***
DBF	**0.32**	**0.33**	**0.30**	**0.31**	**0.33**
	<0.001	***<0.001***	***<0.001***	***<0.001***	***<0.001***
	0.29	**0.32**	**0.25**	**0.23**	**0.31**
	<0.001	***<0.001***	***<0.001***	***<0.001***	***<0.001***
MF	**0.60**	**0.61**	**0.26**	**0.58**	**0.73**
	<0.001	***<0.001***	***0.02***	***<0.001***	***<0.001***
	0.63	**0.66**	**0.38**	**0.48**	**0.74**
	<0.001	***<0.001***	***0.002***	***0.004***	***<0.001***
OSH	0.01	0.00	0.03	0.01	0.00
	>0.10	*>0.10*	*>0.10*	*>0.10*	*>0.10*
	0.05	0.05	0.08	0.06	0.02
	>0.10	*>0.10*	*>0.10*	*>0.10*	*>0.10*
WS	**0.23**	0.10	0.046	0.08	0.05
	0.01	*>0.10*	*>0.10*	*>0.10*	*>0.10*
	0.28	**0.31**	**0.34**	**0.27**	0.14
	0.004	***0.003***	***0.001***	***0.005***	*0.05*
Gr	0.04	0.03	0.04	0.06	0.03
	0.08	*>0.10*	*0.07*	*0.05*	*>0.10*
	0.07	0.08	0.08	0.07	0.05
	0.02	*0.013*	*0.01*	*0.02*	*0.06*

For each biome, the first row indicates the relationships of gNDVI with $T_{\max}$, and the second row indicates the relationships of gNDVI with $T_{\min}$; in each row, the top and bottom numbers are R^2 and P-value, respectively. P-values are denoted in italics. Cells with $R^2 \geq 0.2$ and significant at $P \leq 0.05$ are shown in bold.

ENF, Evergreen Needleleaf Forest; DBF, Deciduous Broadleaf Forest; MF, Mixed Forest; OSH, Open Shrubland; WS, Woody Savanna; Gr, Grassland.

biomes considered here are consistent with other studies based on both NDVI (Davenport & Nicholson, 1993; Paruelo & Lauenroth, 1995) and ANPP measurements (Sala *et al.*, 1988; Knapp & Smith, 2001). These findings suggest that geographic reorganization of long-term averages in precipitation may influence the spatial distribution of productivity within biomes.

Although summer rainfall can be critical to plant life cycles in arid regions (Pake & Venable, 1995, 1996) spatial gradients in late-season rainfall were not responsible for geographic patterns of annual productivity within any biome. Precipitation was far more important in spring, fall, and winter periods when evapotranspirative demand is low, and ground water recharge is most efficient (Webb *et al.*, 1978; Neilson *et al.*, 1992; Paruelo & Sala, 1995). This pattern was especially apparent for spring, when precipitation provides near-surface soil moisture early in the growing season, and also replenishes ground water.

For deeply rooted vegetation types in particular, ground water provides a buffer against soil-water deficits during the growing season (Webb *et al.*, 1978; Woodward, 1987; Stephenson, 1990; Jobbágy & Sala, 2000). Our findings reinforce the importance of water-balance as a primary determinant of spatial gradients in productivity (e.g. Walker & Noy-Meir, 1982; Eagleson & Segarra, 1985; Neilson, 1995) and further suggest that these processes are important for both deep- and shallow-rooted vegetation types.

The dominance of spring precipitation in explaining Grassland productivity reflects the reliance of shallow-rooted life forms on water from the upper soil horizons where early season soil moisture can sufficiently be maintained by precipitation (Walter, 1971; Jobbágy & Sala, 2000). Further, inputs to surface soil water are most critical during early life stages of germination and root development, especially for annual grasses and herbs common to many grasslands ecosystems (Neilson *et al.*, 1992; Pake & Venable, 1995, 1996). The geographic distributions of the two subgroups within the Grassland biome largely reflect changes in grassland productivity along orographic precipitation gradients (e.g. Great Basin steppe to montane forests) as well as synoptic-scale precipitation gradients (e.g. central forest/grassland transition zone) (Ricketts *et al.*, 1999).

In dry regions, where plants can develop and senesce rapidly in response to moisture availability, precipitation-driven pulses in productivity for Grassland may have occurred below the temporal resolution of the data used in this study. This could be the case for Woody Savanna and Open Shrubland as well, which can include substantial herbaceous components. Thus, summer precipitation is possibly more critical to plant productivity for these biomes than is suggested by our results.

The relationship between gNDVI of Woody Savanna and spatial gradients in precipitation supports the view of savannas as tree–grass complexes, with lateral and vertical competition for limited soil water determining tree cover (Walker & Noy-Meir, 1982; Eagleson & Segarra, 1985; Neilson *et al.*, 1992; Pan *et al.*, 2002). Such relationships have obvious implications for the productivity and distribution of savannas under changing precipitation regimes (Haxeltine *et al.*, 1995; VEMAP Members, 1995). However, the absence of associations between gNDVI and precipitation within geographic subgroups of Woody Savanna implies that overstory productivity is not limited by water in this biome type, at least at the regional scale. This suggests that factors other than water limitation, such as

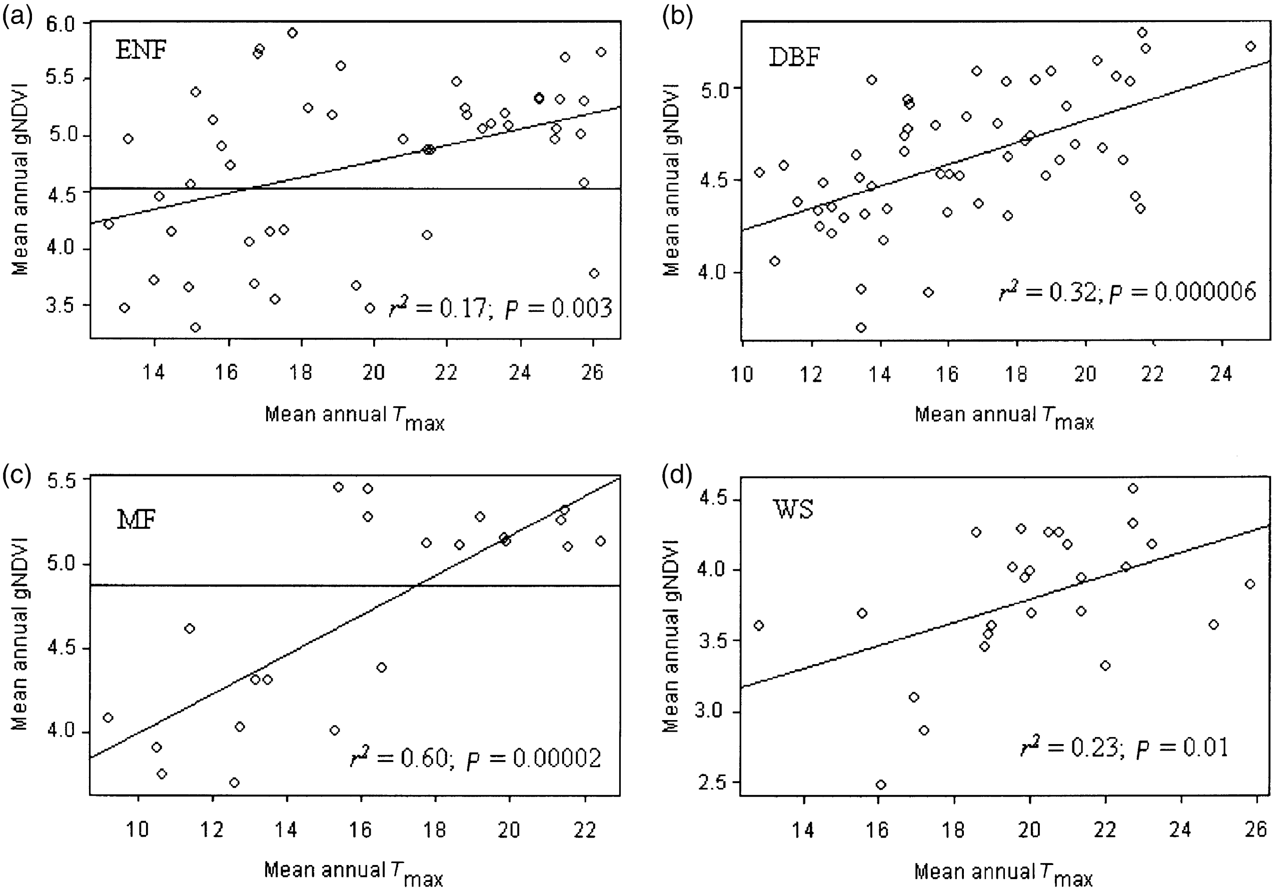

Fig. 5 Relationships between 11-year means of gNDVI and annual average T_{max} for four biomes: (a) Evergreen Needleleaf Forest (ENF); (b) Deciduous Broadleaf Forest (DBF); (c) Mixed Forest (MF); (d) Woody Savanna (WS). Horizontal and vertical lines within plots correspond with Figs 2 and 4.

disturbance (Daly *et al.*, 2000; Van Langevelde *et al.*, 2003) are critical for the development and maintenance of certain savanna complexes. However, we note that gNDVI (and other remote sensing products) may be relatively insensitive to productivity of the shallow rooted, understory vegetation in Woody Savanna.

As with Woody Savanna, similar results for subgroups within Mixed Forest and Evergreen Needleleaf Forest also reflect the buffering effect of ground water for deep-rooted biomes (Neilson *et al.*, 1992; Prentice *et al.*, 1992; Paruelo & Lauenroth, 1996). These results reinforce the value of stratifying functional vegetation types by ecoregion, climate division, or other strata, as an effective means to maintain within-class homogeneity for incorporating vegetation heterogeneity in climate models and modeling vegetation response to climate changes (e.g. VEMAP members, 1995; Bachelet *et al.*, 2001).

Interannual variability in gNDVI and precipitation. Open Shrubland and some grasslands that exist in arid regions are often assumed to experience unusually high interannual variability in rainfall totals (Pake & Venable, 1995, 1996; Davidowitz, 2002). Our results show that, within these biomes, different stations experienced a wide range of interannual variability in precipitation, which was positively correlated to variability in gNDVI. Similar findings have been reported previously for arid biomes (Le Houerou *et al.*, 1988; Kawabata *et al.*, 2001) and for shrubland ecosystems in particular (Paruelo & Lauenroth, 1998).

Variability in productivity for arid biomes was most sensitive to precipitation variability in summer and fall, when water is limiting, and when particularly wet periods may initiate or amplify productivity of late-season grasses and drought-dormant annuals. The potential impact of changes in precipitation variability on the distribution and function of arid vegetation types is most likely mediated by life form. Thus, greater interannual variability in summer precipitation should favor more deeply rooted shrubs that are capable of surviving and growing during dry periods. It is

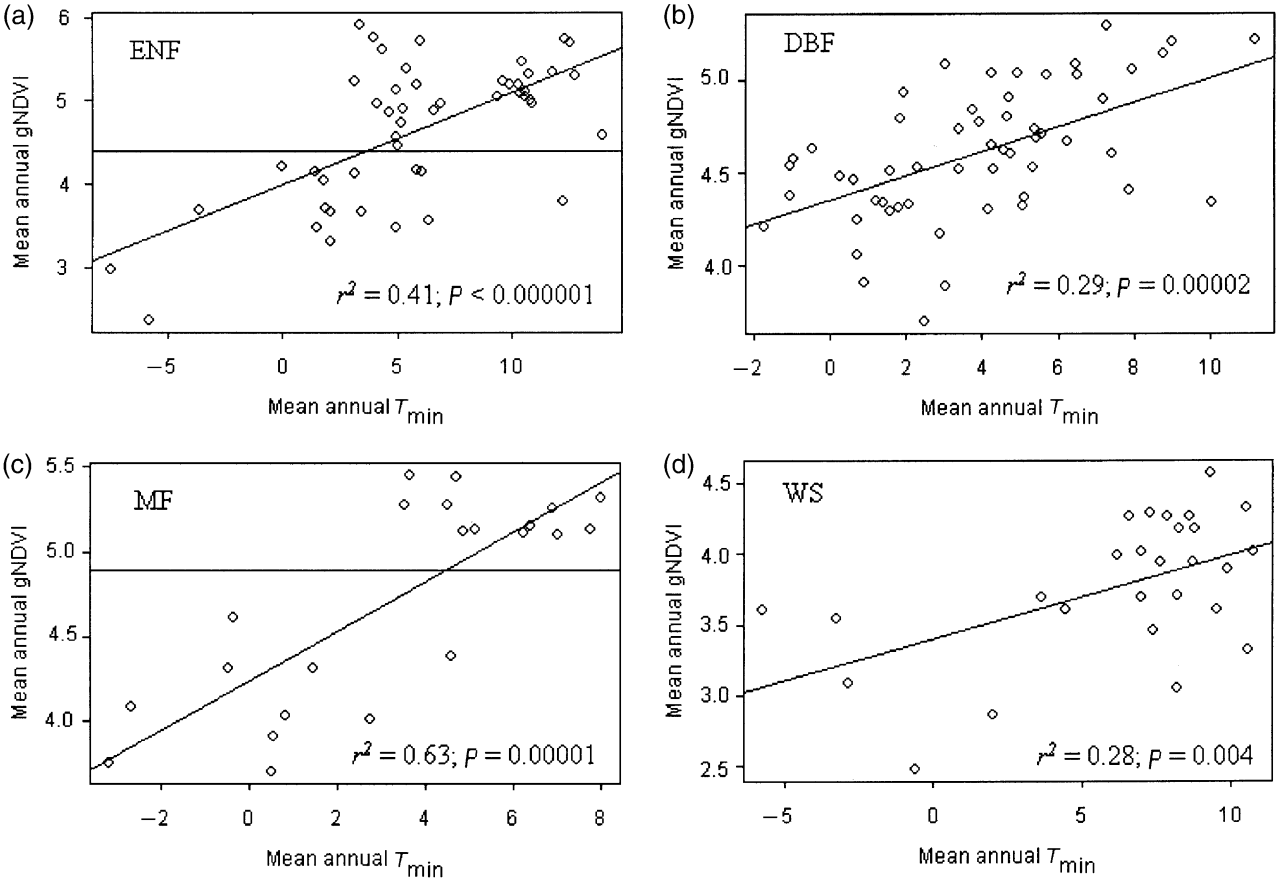

Fig. 6 Relationships between 11-year means of gNDVI and annual average $T_{\min}$ for four biomes: (a) Evergreen Needleleaf Forest (ENF); (b) Deciduous Broadleaf Forest (DBF); (c) Mixed Forest (MF); (d) Woody Savanna (WS). Horizontal lines correspond with Figs 2, 4, and 5.

conceivable that, in the absence of fire or other events that suppress the development of shrublands, increasing interannual variability in precipitation may facilitate shrub proliferation in grasslands.

Long-term means of gNDVI, T*min, and* T*max.* The sensitivity of gNDVI to long-term annual and seasonal averages of $T_{\max}$ and $T_{\min}$ decreased along a bioclimatic gradient, from forested to arid biomes. The lack of association between gNDVI and temperature for Grassland and Open Shrubland, in combination with the results discussed above indicates the dominance of water balance (Jobbágy & Sala, 2000) as the limiting control on productivity in these biomes. For forested biomes, strong positive relationships between productivity and temperature emphasizes the importance of growing-season length in controlling productivity. Our results most likely reflect the synchrony between latitudinal gradients in temperature and productivity, the strength of which increases with decreasing water limitation. The notable sensitivity of Evergreen Needleleaf Forest to winter temperatures, and $T_{\min}$ in particular, may reflect a temperature control on photosynthetic rate, rather than growing-season length. Our results clearly suggest that long-term temperature changes will differentially influence productivity for different biome types (Los *et al.*, 2001) but response to the seasonal component of these changes are difficult to ascertain, potentially due to the strong multicollinearity between the temperature measures used.

Global mean surface air temperature has shown a narrowing of the diurnal temperature range (Karl *et al.*, 1995; Easterling *et al.*, 1997) with global minimum temperatures increasing at about twice the rate of maximum temperatures (IPCC, 1996, 2001). However, the relative ecological consequences of changes in $T_{\min}$ and $T_{\max}$ are largely unexplored over large spatial scales (Alward *et al.*, 1999; Mitchell & Csillag, 2001). Our results suggest that productivity may respond more strongly to changes in $T_{\min}$ for Evergreen Needleleaf Forest and Woody Savanna. Increases in

Table 4 R^2 and P-values of relationships between CV of gNDVI and CV of annual and seasonal averages of $T_{\max}$ and $T_{\min}$

IGBP class	Annual	Spring	Summer	Fall	Winter
ENF	0.00	0.04	0.01	0.00	0.05
	>0.10	*>0.10*	*>0.10*	*>0.10*	*>0.10*
	0.04	0.02	0.01	**0.16**	0.06
	>0.10	*>0.10*	*>0.10*	***0.004***	*0.009*
DBF	0.05	**0.12**	0.04	**0.17**	**0.15**
	>0.10	***0.006***	*>0.10*	***0.001***	***0.002***
	0.10	0.03	0.03	0.02	0.02
	0.017	*>0.10*	*>0.10*	*>0.10*	*>0.10*
MF	0.20	**0.32**	0.04	0.04	**0.43**
	0.037	***0.007***	*>0.10*	*>0.10*	***0.0009***
	0.49	**0.45**	0.06	0.17	**0.30**
	0.003	***0.0007***	*>0.10*	*0.006*	***0.008***
OSH	0.00	0.01	0.04	0.00	0.02
	>0.10	*>0.10*	*>0.10*	*>0.10*	*>0.10*
	0.01	0.01	0.00	0.00	0.00
	>0.10	*>0.10*	*>0.10*	*>0.10*	*>0.10*
WS	0.01	**0.27**	0.09	0.07	0.09
	>0.10	***0.005***	*>0.10*	*>0.10*	*>0.10*
	0.28	0.12	**0.34**	**0.23**	0.07
	0.004	*0.08*	***0.001***	***0.01***	*>0.10*
Gr	0.01	0.00	0.00	0.00	0.04
	>0.10	*>0.10*	*>0.10*	*>0.10*	*>0.10*
	0.00	0.02	0.00	0.01	0.00
	>0.10	*>0.10*	*>0.10*	*>0.10*	*>0.10*

For each biome, the first row indicates the relationships of gNDVI with $T_{\max}$, and the second row indicates the relationships of gNDVI with $T_{\min}$; in each row, the top and bottom numbers are R^2 and P-value, respectively. Cells that are significant at $P \leq 0.05$ are shown in bold. P-values >0.05 and P-values ≤ 0.05 are denoted in italics and bold italics, respectively.

ENF, Evergreen Needleleaf Forest; DBF, Deciduous Broadleaf Forest; MF, Mixed Forest; OSH, Open Shrubland; WS, Woody Savanna; Gr, Grassland.

$T_{\min}$ may thus contribute to increases in productivity within these biomes, which could potentially include increases in stem density.

Across-biome relationships between gNDVI and climate

Most of the variance in average gNDVI across biomes is explained by average annual or seasonal precipitation. Average gNDVI for Evergreen Needleleaf Forest was high given the average amount of summer precipitation (Fig. 7c) and summer $T_{\max}$ (Fig. 8), and low given the amount of winter precipitation (Fig. 7e). These residuals suggest an especially strong reliance of Evergreen Needleleaf Forest on stored water supplies rather than growing-season precipitation, and identify water balance as a potentially limiting factor for this biome (Webb *et al.*, 1978; Stephenson, 1990).

Table 5 Biome-level means of gNDVI (unitless), precipitation (mm), $T_{\max}$ (°C), and $T_{\min}$ (°C)

	ENF	DBF	MF	OSH	WS	Gr
GNDVI	4.67	4.61	4.72	1.75	3.77	3.04
	0.83	*0.36*	*0.61*	*0.51*	*0.50*	*0.52*
MAP	1268.88	1141.78	1143.44	284.98	856.72	522.71
	540.35	*159.57*	*332.01*	*77.42*	*372.42*	*248.05*
Annual $T_{\min}$	6.07	3.89	3.31	6.19	6.14	3.43
	4.74	*2.94*	*3.30*	*6.03*	*4.46*	*4.26*
Annual $T_{\max}$	19.29	16.35	16.16	22.10	20.36	18.19
	4.70	*3.41*	*4.05*	*4.89*	*3.20*	*4.08*
Summer $T_{\min}$	13.22	14.47	13.91	15.27	15.96	13.80
	5.39	*2.51*	*2.64*	*6.13*	*4.76*	*4.21*
Summer $T_{\max}$	28.32	27.52	26.96	32.87	30.89	29.95
	4.16	*2.44*	*2.73*	*4.14*	*3.08*	*3.10*
Winter $T_{\min}$	−0.28	−6.28	−6.84	−1.87	−3.11	−6.35
	4.77	*4.02*	*5.10*	*5.85*	*5.12*	*5.00*
Winter $T_{\max}$	10.14	4.63	4.70	11.53	9.47	6.40
	5.58	*4.44*	*5.69*	*5.39*	*4.06*	*5.53*

Standard deviations are denoted in italics.

ENF, Evergreen Needleleaf Forest; DBF, Deciduous Broadleaf Forest; MF, Mixed Forest; OSH, Open Shrubland; WS, Woody Savanna; Gr, Grassland; MAP, mean annual precipitation.

The strong relationships between gNDVI and precipitation totals from spring and fall further emphasize the importance of rainfall during the beginning and end of the growing season in driving differences in productivity across biomes. In combination with the negative association between mean annual gNDVI and mean summer $T_{\max}$, our results reflect an interaction between the seasonality characteristics of precipitation and temperature in governing the distributions of biomes, presumably due to their joint control over annual soil-water budgets (Stephenson, 1990).

Sources of uncertainty

There are several uncertainties related to the data and methods used in this analysis that may influence the results presented here. First, NDVI is not as effective an indicator of photosynthetic activity for sites with sparse vegetation. Second, despite corrections for most known, systematic sources of error (Eidenshink, 1992) the satellite data used in this study contain variability in radiometry that is related to instrument, orbital, or atmospheric characteristics. Moreover, uncertainties in the geolocation of AVHRR pixels can result in mismatches between the locations of climate stations and their enclosing pixels. By using a large number of stations, and averaging over a number of years, we

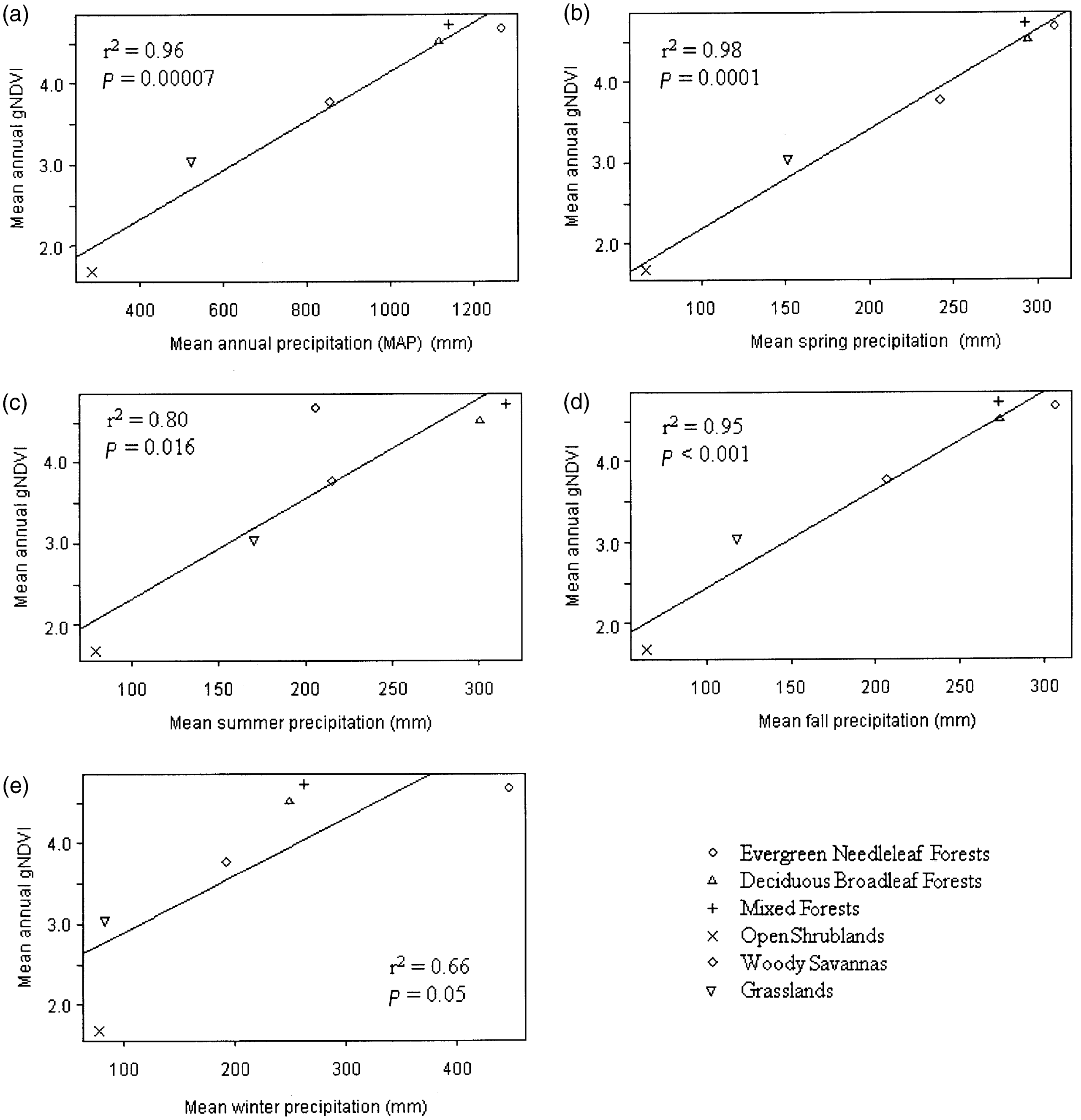

Fig. 7 Relationships between biome-level means of gNDVI and annual and seasonal precipitation across six biomes: (a) annual; (b) spring; (c) summer; (d) fall; (e) winter.

have attempted to limit the impact of this effect on the results. Finally, the approach used to derive the growing season will have overestimated productivity in cases where NDVI never drops below 0.1. Such cases are most likely to occur for Evergreen Needleleaf Forest or Mixed Forest, and could influence the across-biome results by elevating the points for these two class types along the *y*-axis in Fig. 7.

Because there is a large amount of structural and compositional variability within biomes, the degree to which pixels are consistently classified using satellite data is difficult to determine over large areas. For example, a comparison of the 1993 AVHRR-based map used in this analysis with the 2000/2001 MODIS-based map that also uses the IGBP land-cover taxonomy (Friedl *et al*., 2000) produces an agreement rate of only

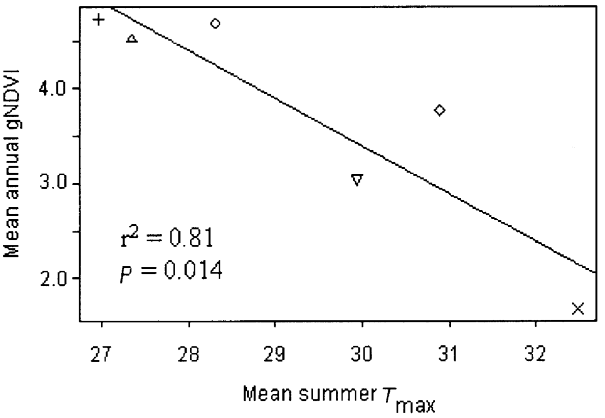

Fig. 8 Relationship between mean annual gNDVI and mean summer T_{max} across six biomes.

50.1% (Table 1) (unpublished results). Confusions are particularly common between Deciduous Broadleaf Forest and Mixed Forest; and between Open Shrubland and Grassland. These disagreements can result from land-cover changes, misclassification in one or both maps, or misregistration between them. We reran our analyses using only stations for which the two maps agreed. The results changed marginally in magnitude, with no changes in sign. However, with loss in degrees of freedom (Table 1) some of the resulting statistics became insignificant.

Conclusion

Our results reflect the seasonal climatic control over large-scale spatial gradients in plant productivity, both within and across biomes. Correlations between precipitation and approximated plant productivity differed across biomes in a manner consistent with their expected sensitivity to soil-water limitation. For example, productivity of relatively shallow-rooted, drought-prone ecosystems, such as Grassland and Open Shrubland, varied strongly with gradients in spring precipitation. Conversely, winter precipitation, presumably due to a greater contribution to stored water, was more important for deep-rooted forest biomes, especially Evergreen Needleleaf Forest, which is more typically water limited.

In contrast to water balance, which influenced productivity for all biomes, the effect of seasonal T_{max} and T_{min} was only apparent for forested biomes, which are less likely to be water limited. The seasonality of temperature relations, and the relatively greater importance of T_{min} for some biomes, suggest that the dominant effect of temperature is through its influence on growing-season length.

Historically, the increase in US annual precipitation is due largely to increases during fall (September–November) (Groisman & Easterling, 1994; IPCC, 1996), which is related to gNDVI for the more arid biomes considered here. As with spring precipitation, late season contributions to soil moisture can extend the growing season for water-limited biomes, such as Open Shrubland and Grassland. These sensitivities may lead to changes in the density or extent of woody vegetation in arid and semi-arid regions, with consequent implications for ecosystem productivity and carbon storage (Brown *et al.*, 1997; Goodale & Davidson, 2002; Jackson *et al.*, 2002).

Our results indicate that the greatest climate-change impacts on biome distributions and productivity would result from changes in spring, winter, and fall precipitation, and changes in fall and spring temperature, especially T_{min}, which has historically increased at roughly twice the rate of T_{max} (IPCC, 2001). These effects differ by biome type, and also vary within biomes.

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