The Response of Global Terrestrial Ecosystems to Interannual Temperature Variability

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Measurements of atmospheric carbon dioxide and satellite-derived measurements of temperature and the vegetation index were used to investigate relationships among climate, carbon dioxide, and ecosystems. At the global scale, lagged correlations between temperature and carbon dioxide growth rate were found, indicating modulation by biogeochemical feedbacks. Spatial analysis of the temperature and vegetation index data suggests that the global correlations are a composite of individualistic responses of different ecosystems. The existence of biome-specific time scales of response implies that changes in global ecosystem distributions could indirectly alter the relationships between climate and carbon storage.

In analyses of global change, predicting terrestrial carbon exchange is crucial (*1*, *2*). If biospheric carbon storage increases, anthropogenic emissions will be offset (*3*). However, if terrestrial carbon is lost to the atmosphere, climate change could be exacerbated and mitigation costs increased (*2*, *4*, *5*). Ecosystem models have previously been used to project changes in the terrestrial carbon cycle, but their predictions differ in magnitude and sometimes in the sign of their response (*1*, *4*). Here, we examined the atmospheric CO_2 record along with global, satellite-derived temperature and vegetation index data in order to gain insight into the mechanisms controlling the response of terrestrial carbon storage to climate variability.

A number of recent analyses that used global measurements of the concentrations of atmospheric CO_2, its isotopes, and O_2 have demonstrated the importance of the terrestrial biosphere in the global carbon cycle (*6*–*8*). Both immediate and delayed temperature responses can be seen in the atmospheric CO_2 record and have been attributed to the activity of terrestrial vegetation (*7*–*9*). Because trends are difficult to discern unambiguously with the existing time series observations, we focus on the issue of interannual variability as a means to understand controls over CO_2 exchange.

We used three data sets to independently evaluate the hypothesis (*10*) that terrestrial ecosystems exhibit complex behavior on interannual time scales in response to climatic perturbations. The measurements consisted of atmospheric CO_2 concentration data from flask samples, collected by the Climate Monitoring and Diagnostics Laboratory (CMDL) (*11*), and two global remote sensing measurements: lower tropospheric temperature anomalies detected by the microwave sounding unit (MSU) (*12*) and the normalized difference vegetation index (NDVI) (*13*) from the advanced very high resolution radiometer (AVHRR). The data sets are documented elsewhere (*11*–*14*), and we applied some additional processing to facilitate the analysis.

Monthly averaged CO_2 growth rates (1979 through 1994) were calculated for two stations, Mauna Loa, Hawaii (MLO), and the south pole (SPO), by taking the first difference of the time series. We then removed the seasonal cycle in a similar fashion to Keeling *et al.* (*9*) by fitting a fourth-order harmonic function and smoothing the data with a 3-month moving window (*15*). The gridded satellite data were spatially and temporally reaggregated to a common global 1° by 1° grid with a time interval of 1 month (*16*). For all three data sets, statistically significant trends, if present, were removed to produce approximately stationary time series.

We calculated autocorrelograms and pairwise cross correlograms of monthly global and hemispheric mean temperature, NDVI, and CO_2 growth rate, defining the lags such that temperature always led the other variables, and such that NDVI led CO_2 growth rate. Regional-scale ecosystem changes can affect climate, but the direction of causality we consider (temperature effects on ecosystems) shall be the most significant on the time and space scales discussed here. Lagged correlations could arise either from coordinated temperature-precipitation changes or, spuriously, from periodicities in the data. The autocorrelation functions for all three variables (temperature, CO_2, and NDVI), however, decrease steadily on time scales less than 4 years, with apparent oscillatory behavior emerging only on longer time scales, perhaps associated with the El Niño–Southern Oscillation (*17*). Also, the quasi-periodic behavior of the temperature autocorrelations occurs at time scales that are incompatible with the observed lagged correlations (Figs. 1 and 2). Precipitation anomalies are usually more localized than temperature anomalies, thus their global effect on lagged correlations is unlikely but cannot be rigorously excluded.

A significant relationship between CO_2 growth rate and temperature can be seen in Fig. 1A, centered around a 2-year lag. A positive NDVI anomaly with a similar time delay is shown in Fig. 1B. These apparent lagged responses suggest a greater role for indirect versus direct effects of climate on net ecosystem carbon exchange. Keeling *et al.* (*7*) suggested that such a response could have been responsible for a negative CO_2 anomaly that began before the Mount Pinatubo eruption in 1991 and continued downward until late 1993. Terrestrial responses to

Table 1. Vegetation classes (*18*) used in the spatial analysis to determine significant interannual lags in NDVI response to temperature. Class numbers are referred to in Figs. 2 and 3.

Class	Dominant vegetation type	Number of pixels	Area (10^6 km^2)
1	Broadleaf evergreen	1098	13.42
2	Broadleaf deciduous	320	3.30
3	Mixed coniferous/broadleaf and woodland	769	6.60
4	Coniferous and woodland	2018	12.99
5	High latitude deciduous and woodland	952	5.75
6	Tundra	1528	7.09
7	C4 grassland	779	8.93
8	C4 wooded grassland	1457	17.10
9	Shrubs and bare ground	1035	11.00
10	C3 grassland	1255	11.52
11	C3 wooded grassland	454	4.59
12	Cultivation	1370	13.28

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temperature changes appear to result in either enhanced plant production, reduced heterotrophic respiration, or both, such that global net ecosystem production is positive about 2 years after a warm anomaly. Conversely, a cool anomaly should lead to reduced terrestrial uptake.

In a second experiment, we examined the temperature-NDVI correlations spatially, using annual averages of the two satellite data sets. The data were aggregated into global land cover classes according to the map of DeFries *et al.* (*18*) (Table 1). Within each class, and for each year, multiple linear regressions of NDVI anomaly against temperature anomaly were performed, yielding correlations between the spatial patterns of the two variables. The dependent variable in the regression was "current" NDVI, and the independent variables were temperature in the previous year, temperature in the last year, and so on (*19*). Thus, we treated within-class pixels as replicate measurements. Regression coefficients b_i (slopes) were estimated for each biome and for each year that represent the current and lagged ecosystem sensitivity to temperature anomalies but are not affected by year-to-year changes in the mean (*20*). This technique is an alternative to direct time-series comparisons (Fig. 1), guided by the assumption that spatially adjacent ecosystems, which are also morphologically and physiologically similar, manifest similar responses to temperature.

The spatial method requires some special considerations. Pooled within-biome data are not independent because of their proximity to one another. Therefore, we accounted for the spatial autocorrelation in the data by estimating regression coefficients using the method of weighted least squares (*21*, *22*) to avoid spuriously high correlations. The weights were determined from an estimated semivariogram (*23*) of the residuals for each biome class. In addition to spatial correlations, there potentially exists temporal autocorrelation between the independent (lagged temperature) variables, so we performed a "backward" stepwise variable selection process (*24*).

The spatio-temporal analysis of the temperature and NDVI data (*19*, *22*, *24*) reveals correlations on all of the time

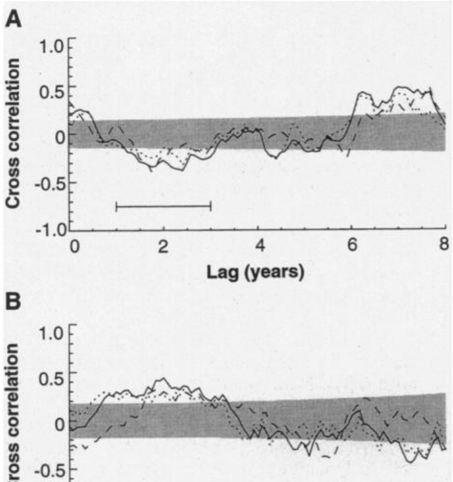

Fig. 1. Cross-correlation functions for lagged temperature versus (**A**) atmospheric CO_2 growth rate and (**B**) NDVI. In both panels, the solid line represents global mean (area-weighted) values, the dashed line represents the Southern Hemisphere correlations, and the dotted line, the Northern Hemisphere correlations. Outside the shaded region, values are significantly ($P < 0.05$) different from zero. Within the bracketed period (1 to 3 years), both CO_2 and NDVI are weakly correlated with lagged temperature. We focus on these time scales in the spatial analysis (Figs. 2 and 3).

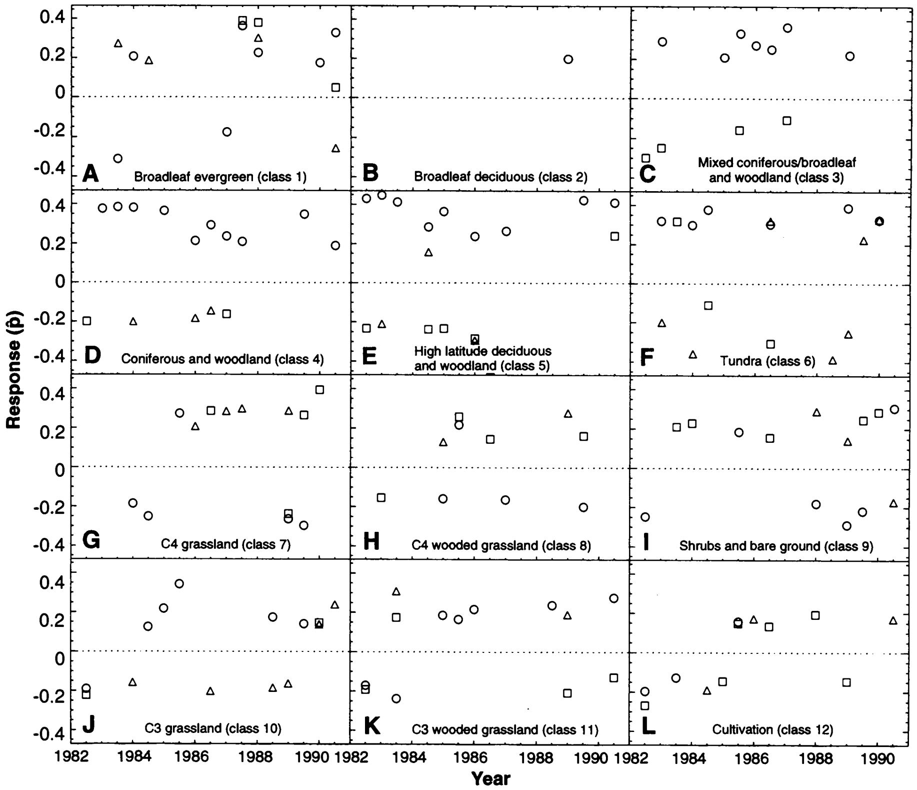

Fig. 2. (**A** to **L**) Statistically significant ($P < 0.05$) standardized regression coefficients of a multiple linear regression of current NDVI on present (zero lag) and past (1- and 2-year lag) temperature. Circles, zero lag; triangles, 1-year lag; squares, 2-year lag. The regressions were performed spatially, and within biome, for each year by using annual mean NDVI and temperature anomalies, with means centered on 6-month intervals. The data were corrected to exclude snow cover and below-freezing temperatures. The coefficients (slopes) $\hat{\rho}$ represent the relative spatial variation in NDVI anomaly associated with spatial variation in past or present temperature anomaly. Correlation coefficients are typically low, and insignificant slopes are not plotted.

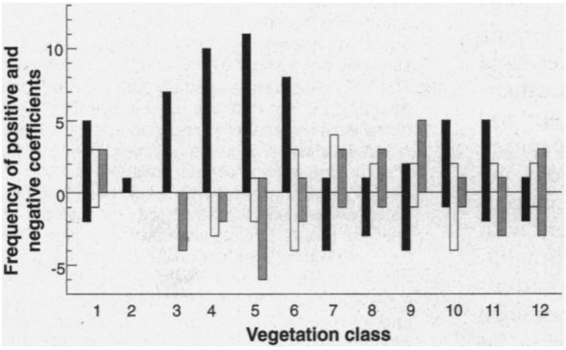

Fig. 3. Frequency of either positive or negative significant correlation coefficients for the spatial regression of NDVI versus lagged temperature (Fig. 2). Negative values indicate the number of significant anticorrelations. The vegetation classes are listed in Table 1. Black bars represent zero lag, white bars represent a 1-year lag, and gray bars represent a 2-year lag.

scales analyzed (0 to 2 years). Significant lagged correlations were nearly as frequent as immediate (*25*) correlations (Fig. 2), and patterns of correlation varied significantly between ecosystems. Temperate and boreal regions tended to show positive zero-lag correlations, indicating an initial positive response to warmer conditions (or negative response to colder conditions), often followed by negative lagged correlations (Fig. 3). In contrast, tropical and arid ecosystems often showed negative initial correlations, indicating reductions in NDVI during warm years. This contrast suggests that, whereas NDVI (and by extension, vegetation activity) responds directly and positively to temperature anomalies in colder ecosystems, temperature may have direct negative effects on plant growth, or may increase water stress in semiarid ecosystems (classes 7, 8, and 9 in Fig. 3). Note that C3 (temperate) and C4 (semiarid and tropical) grasslands and savannas have opposite zero-lag correlations (Fig. 3; classes 7 and 8 compared with classes 10 and 11). Thus, regional climate anomalies occurring in different ecosystems could have qualitatively different effects on global CO_2.

Lagged correlations are frequently of opposite sign to the immediate (same year) correlations. This may arise from a tradeoff between plant and microbial activity. Changes to plant growth affect the input of biomass to heterotrophic microorganisms as leaves and roots are shed seasonally. Increases (decreases) in biomass inputs in a given year, resulting from temperature anomalies, could cause increased (decreased) microbial competition for nutrients and reduced plant growth in subsequent years, producing the pattern of correlation and lagged correlation in most ecosystem types (Fig. 3) (*10, 26*). Analogous delayed effects due to long turnover times of deep soil moisture are also possible (*27*).

The coordinated lags in monthly NDVI and CO_2 growth rate anomalies with temperature suggest that, at the global scale, increased plant growth removes additional CO_2 from the atmosphere 1.5 to 2 years after warm anomalies, while absorbing lower than average amounts after cold anomalies. Although the data we evaluated do not directly implicate nutrient and water cycling, the lags in the temperature versus CO_2 and NDVI correlations are consistent with the time scales of biogeochemical regulation and inconsistent with instantaneous physiological adjustment. The biome-level responses show that, although global correlations exist, they are a composite of individualistic responses at different locations and also reflect the spatial structure of climate anomalies. This diversity of terrestrial response to temperature implies that if the global distribution of ecosystems were to change, the response of the biosphere to climate could be altered (*4*).

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14. All three data sets are available over the World Wide Web: ghrc.msfc.nasa.gov (MSU temperature anomaly data); xtreme.gsfc.nasa.gov (AVHRR data); and www.cmdl.noaa.gov (flask CO_2 data).
15. Removing the seasonal component of this data requires Fourier decomposition because the annual cycle of the CO_2 measurements represents a superposition of amplitude and phase of vegetation activity distributed over each hemisphere. We produced a global mean monthly CO_2 growth rate time series by averaging the MLO and SPO curves (*9*).
16. The MSU temperature anomaly data are produced on a 2.5° by 2.5° grid. We used a global 1° by 1° digital elevation model to apply an adiabatic lapse rate adjustment and create a corresponding 1° by 1° temperature anomaly map. We chose 1° by 1° degree to be consistent with the global vegetation database we used to characterize biome-specific relations (Table 1). Data were available from 1979 to 1994, with a base period for the annual cycle defined as 1982 to 1991. We used the base annual cycle and a temperature climatology [R. Leemans and W. Cramer, *The IIASA Database for Mean Monthly Values of Temperature, Precipitation, and Cloudiness on a Global Terrestrial Grid* (International Institute for Applied System Analysis, report RR-91-18, 1991)] to adjust the anomalies to reflect biologically meaningful temperature variations, setting temperatures less than 0°C equal to 0°C to emphasize growing season anomalies. We constructed NDVI anomalies by similarly truncating negative values (typically, for vegetated surfaces, $0 < \text{NDVI} < 0.7$) and subtracting the mean annual cycle for the period 1982 to 1990. We limited our use of AVHRR data to this period because the aerosols released by the Mount Pinatubo eruption in 1991 caused persistent global reductions in atmospheric optical depth, noticeably corrupting the NDVI signal.
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19. Formally, $\mathbf{Y} = \mathbf{X}\mathbf{b} + \varepsilon$, where $\mathbf{X}$ is a matrix constructed from the temperature anomalies in year t, $t - 1$, $t - 2$, and so on, $\mathbf{Y}$ is the column vector containing the dependent variable, NDVI, $\mathbf{b}$ is a vector of regression coefficient, and ε is a vector of residuals.
20. Though spatial and temporal averaging of NDVI reduces errors associated with small-scale spatial and temporal variability, low-frequency contamination remains and is associated with atmospheric composition (principally, aerosols and water vapor), orbital drift, and instrument changeover. We applied a simple adjustment to correct for satellite orbital drift and the changeover from NOAA9 to NOAA11 [C. J. Tucker, W. W. Newcomb, H. E. Dregne, *Int. J. Remote Sens.* **15**, 3547 (1994)], but this bias adjustment is on the order of year-to-year changes in NDVI, usually 0.01 to 0.06 units.
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22. The coefficient estimates are given by $\hat{\mathbf{b}} = (\mathbf{X}^t\Omega^{-1}\mathbf{X})^{-1}\,\mathbf{X}^t\Omega^{-1}\mathbf{Y}$, where Ω is the variance covariance matrix of the residuals ε_i in (*26*) taken from estimated semivariograms.
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24. The resultant regression model retains the combination of $\hat{b}_i$ terms (if any) corresponding to significant ($P < 0.05$, F test of the hypothesis $\hat{\mathbf{b}} = 0$) 0-year, 1-year, or 2-year lags. Standardized coefficients $\hat{\mathbf{p}}$ were obtained by the transformation $\hat{p}_i = \hat{b}_i S_i / S_\mathbf{Y}$ (for $i = 0, 1, 2$), where S_i denotes the standard deviation of the ith lagged independent variable X_i, and $S_\mathbf{Y}$ is the standard deviation of the vegetation index values $\mathbf{Y}$. Thus, we present coefficients $\hat{\mathbf{p}}$ (Fig. 2) that are a "commensurate measure of response" of NDVI to temperature [S. Selvin, *Practical Biostatistical Methods* (Duxbury, Belmont, CA, 1995)].
25. "Immediate," in this context, implies phenomena that appear in the data during the same averaging period (1 year).
26. The changes in CO_2 growth rate at these time scales reflect changes to global net ecosystem production (NEP, which is equal to net primary production minus heterotrophic respiration). Because temperature affects both plant and microbial physiology similarly, the instantaneous response of NEP to temperature reflects the small asymmetry in the temperature responses of autotrophs and heterotrophs.
27. J. S. Famiglietti, personal communication.
28. We acknowledge helpful suggestions from P. Tans, C. J. Tucker, R. Myneni, G. Asrar, J. L. Privette, T. R. Seastedt, F. S. Chapin, and three anonymous reviewers. We thank the participants of the *Seventh Annual Symposium Centre National D'Etudes Spatiales, Physical Measurements and Signals in Remote Sensing*, held in Courchevel, France, 9 to 11 April 1997, for comments on a preliminary version of this work. This research was supported in part by Oak Ridge Associated Universities' Graduate Fellowships for Global Change and NASA [Earth Observing System–Interdisciplinary Science (EOS-IDS)]. The National Center for Atmospheric Research is sponsored by NSF.

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