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Partitioning interannual variability in net ecosystem exchange between climatic variability and functional change

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Summary Interannual variability (IAV) in net ecosystem exchange of carbon (NEE) is a critical factor in projections of future ecosystem changes. However, our understanding of IAV is limited because of the difficulty in isolating its numerous causes. We proposed that IAV in NEE is primarily caused by climatic variability, through its direct effects on photosynthesis and respiration and through its indirect effects on carbon fluxes (i.e., the parameters that govern photosynthesis and respiration), hereafter called functional change. We employed a homogeneity-of-slopes model to identify the functional change contributing to IAV in NEE and nighttime ecosystem respiration (R_E). The model uses multiple regression analysis to relate NEE and R_E with climatic variables for individual years and for all years. If the use of different slopes for each year significantly improves the model fitting compared to the use of one slope for all years, we consider that functional change exists, at least on annual time scales. With the functional change detected, we then partition the observed variation in NEE or R_E to four components, namely, the functional change, the direct effect of interannual climatic variability, the direct effect of seasonal climatic variation, and random error. Application of this approach to a data set collected at the Duke Forest AmeriFlux site from August 1997 to December 2001 indicated that functional change, interannual climatic variability, seasonal climatic variation and random error explained 9.9, 8.9, 59.9 and 21.3%, respectively, of the observed variation in NEE and 13.1, 5.0, 38.1 and 43.8%, respectively, of the observed variation in R_E.

Keywords: CO_2 flux, ecosystem respiration, eddy-covariance measurement, homogeneity-of-slopes model.

Introduction

Among the important findings of long-term flux measurement initiatives under the auspices of FluxNet is the phenomenon of interannual variability (IAV) in net ecosystem exchange (NEE) of CO_2 (Goulden et al. 1996, Bubier et al. 1998, Chen et al. 1999, Griffis et al. 2000, Kelly et al. 2000, Baldocchi et al. 2001, Barford et al. 2001, Falge et al. 2001). For example, NEE determined from eddy-covariance measurements in a 60- to 80-year-old deciduous forest in the northeastern USA ranged from 1.2 to 2.5 Mg C ha^{-1} year^{-1} during the period from 1993 to 2000 (Barford et al. 2001). Observed NEE at a subarctic fen varied from a net source of 76 g CO_2 m^{-2} in 1994 to a net sink of 235 g CO_2 m^{-2} in 1996 (Griffis et al. 2000). Similarly, large IAV has been observed in grasslands (Flanagan et al. 2002), an alpine forest (Monson et al. 2002), and a boreal aspen forest and a black spruce forest in Canada (Arain et al. 2002). The IAV in NEE is a ubiquitous phenomenon observed at almost all of the flux sites across the world (Baldocchi et al. 2001). Understanding the causes of IAV and partitioning the variability into its sources are urgently needed to improve our prediction of global carbon cycling.

Observed IAV in NEE at flux sites has been related to several sources, including: (1) changes in climatic variables, e.g., temperature, cloud cover, summer drought, winter snow depth and the time of snowmelt (Goulden et al. 1998, Griffis et al. 2000); (2) changes in physiological and ecological processes such as growing season length, natural or artificial changes in stand structure, the timing of leaf emergence, and coupling between carbon and nutrient cycling with time delay (Goulden et al. 1996, Chen et al. 1999, Black et al. 2000, Botta et al. 2000, Griffis et al. 2000); and (3) altered balance between canopy photosynthesis and ecosystem respiration (Black et al. 2000, Houghton 2000, Potter et al. 2001, Schimel et al. 2001). Empirical evidence suggests that climatic variability among years is among the factors causing IAV in NEE, which is also strongly influenced by climate-induced changes in ecosystem physiological parameters. However, it is unclear how much variability is attributable to external factors (e.g., climatic variability) and how much to internal factors (photosynthesis and respiration parameter attributes).

The IAV in NEE has been studied empirically and with simulation models. Direct measures of IAV in NEE include differences in mean values, coefficients of variation (Goetz et al. 2000, Houghton 2000, Kelly et al. 2000), range (Savage and Davidson 2001), and relative changes in yearly means (Barford et al. 2001). Such measures provide limited insight into causes of variation. Simulation models have been employed to examine various mechanisms causing IAV in NEE (Potter and Klooster 1998, Goetz et al. 2000, Grant and Nalder 2000, Ito and Oikawa 2000, Knorr 2000, Griffis and Rouse 2001, Katul et al. 2001). The Terrestrial Ecosystem Model, for example, has been applied to the Amazon Basin. It was found that IAV in NEE was largely controlled by variation in soil water content and nutrient availability, which were in turn influenced by yearly changes in precipitation and temperature (Tian et al. 2000). Griffis and Rouse (2001) used an empirical model and concluded that changes in air temperature and timing of precipitation events have a strong influence on NEE. Wilson and Baldocchi (2001) used a biophysical canopy exchange model to predict IAV in NEE from observed changes in canopy structure, climate, soil water content and temperature. Overall, modeling has helped identify major connections between climatic variability, especially extreme climatic events of drought and disturbances, and IAV in carbon fluxes.

In addition to the modeling studies, Katul et al. (2001) recently analyzed the wavelet spectral properties of three scalar fluxes (heat, water vapor, and CO_2) and demonstrated that seasonal variability contributes substantially to the overall variance of these three fluxes. Furthermore, their analysis clearly indicated the need to investigate variability at annual and longer time scales. The present study was designed to examine IAV in NEE and ecosystem respiration (R_E) using long-term eddy-covariance measurements at the Duke Forest AmeriFlux pine site from August 1997 to December 2001.

Here we examine both direct and indirect effects of climatic variability on IAV in NEE and R_E. The ensemble of all indirect effects of climatic variability on carbon fluxes is referred to here as the functional change. We used a homogeneity-of-slopes (HOS) model to detect the functional change of IAV in NEE and R_E. A combination of the separate-slopes model with a multiple regression model was used to estimate the contributions of functional change, interannual climatic variability, seasonal climatic variation and random error to the observed total variation in NEE and R_E. We describe the HOS model, the method of partitioning observed IAV in NEE and R_E into different components, and the overall analytical procedure.

Materials and methods

Site description and data collection

Data were collected from the Duke Free Air CO_2 Enrichment (FACE) experimental site in Orange County, NC (35°58′ N, 79°05′ W). The site is equipped with six FACE rings and one meteorological tower (Hendrey et al. 1999, Katul et al. 1999). The site consists of a 32-ha parcel of even-aged loblolly pine (*Pinus taeda* L.) forest on a clay loam soil. Tree growth in the plantation is relatively uniform, with a median height of 13 m, a mean diameter of ~15 cm and an LAI of ~3.5 (in 1996).

An eddy-covariance system was installed in one ambient CO_2 ring in August 1997 to measure ecosystem CO_2 flux (see Katul et al. 1997, 1999 and Lai et al. 2000 for details). Net ecosystem exchange of CO_2 was measured with an LI-6262 gas analyzer (Li-Cor, Lincoln, NE) until May 2001 and a Li-Cor LI-7500 thereafter, together with a CSAT3 (Campbell Scientific, Logan, UT) triaxial sonic anemometer. Photosynthetically active radiation (PAR) was measured at the canopy top with a Li-Cor LI-190SZ. When a PAR measurement was missing, we used a regression relationship with net radiation (R_n) to “gap-fill” the 30-min mean (PAR = $2.4870R_n + 78.7710$, $r^2 = 0.88$, $n = 14140$). Air temperature (T_A) and wind speed (WS) were measured with the CSAT3 anemometer at the canopy top. Relative humidity (RH) and vapor pressure deficit (VPD) were measured with a Vaisala probe positioned at 2/3 canopy height. Soil temperature (T_S) was measured with thermistors (Siemens GmbH, Nuernberg, Germany) at one point at 10–12 cm depth in each ring. Soil water content (M_S) was measured with four probes in each of the six plots, integrating the upper 30-cm soil layer that encompasses the total root volume at this site (Oren et al. 1998). Leaf area index was measured monthly from August 1996 to December 2001 by optical techniques (Li-Cor LAI-2000).

About 78,000 observations from half-hourly measurements were used to compute daily values of NEE, WS, PAR, T_A, RH, VPD, T_S and M_S. To minimize fluctuations in single-day measurements and to maximize use of observations with partially missing values, we calculated weekly means of daily values by summing half-hourly data over the 24-h period and then averaging the daily sums over seven days (Hui et al. 2001, Wilson and Baldocchi 2001).

Nighttime R_E was calculated by averaging nighttime measurements of NEE from 2030 to 0430 h daily. Nighttime T_A, T_S, M_S and WS were calculated accordingly. Because plant photosynthesis provides substrate for plant respiration, we calculated daytime ecosystem CO_2 exchange (P_D) by averaging measured NEE from 0830 to 1630 h to test if R_E was influenced by P_D. Because intercepted PAR generally showed a better fit than PAR, we calculated intercepted PAR (IPAR) as: IPAR = PAR$(1 - e^{(-\mathrm{LAI}k)})$, where k is canopy light extinction coefficient, equaling 0.52 for a coniferous forest (Pierce and Running 1988), and LAI is measured leaf area index, displaying a strong seasonal variation ranging from 2.63 in January to a maximum of 4.67 in July, and less year-to-year variation (Katul et al. 2001). Daily LAI values were obtained by linear interpolation of the monthly LAI data.

We excluded observations from the analysis if data with one or more individual variables were missing or the mean friction velocity was less then 0.15 m s^{-1}. Data in 1997 started from August and may not be fully comparable with the other years' data, but for the maximum use of available information, we included these data in the analysis. A total of 197 data points was used for the analysis of R_E and 189 for NEE.

Homogeneity-of-slopes (HOS) model

We used the HOS model to detect the effect of the functional change on IAV in NEE and R_E. The HOS model is a regression model, but considers the interaction of climatic variable and year:

$$Y_{ij} = a + \sum_{k=1}^{m} b_k X_{ijk} + \sum_{k=1}^{m} b_{ik} X_{ijk} + e_{ij} \quad (1)$$

where i is the ith year equaling 1, 2, …, y ($y = 5$ in this study); j is the jth day of a year equaling 1, 2, … , n; k is the kth independent variable equaling 1, 2, …, m ($m = 7$ in this study) for IPAR, T_A, T_S, M_S, VPD, RH and WS, respectively; Y_{ij} is a dependent variable, NEE or R_E, observed in the ith year at the jth day; X_{ijk} is an independent variable measured at the jth day of the ith year for the kth variable (called climatic variables hereafter); b_{ik} is the slope that links the interactive term of year and kth climatic variable with NEE or R_E; and e_{ij} is the random error associated with observed values of Y_{ij}.

To examine the existence of the functional change, we tested the null hypothesis (H_0: $b_{ik} = 0$) for all years versus the alternative hypothesis (H_1: $b_{ik} \neq 0$) for any of the years. The significant test was conducted by the F-test, which tests whether using different slopes of a climatic variable for each year can significantly improve the fitting of Equation 1 with observations compared with using only one slope for all years. If H_0 cannot be rejected, none of the slopes "significantly" varies among years. We then assumed that no functional change exists in the ecosystem processes and Equation 1 was simplified to a multiple regression model:

$$Y_{ij} = a + \sum_{k=1}^{m} b_k X_{ijk} + e_{ij} \quad (2)$$

If H_0 is rejected, the slopes of regression lines to relate NEE or R_E with climatic variables vary among years. The functional change is therefore detected through these slopes and Equation 1 was simplified to a separate-slopes model:

$$Y'_{ij} = a + \sum_{k=1}^{m} b_{ik} X_{ijk} + e_{ij} \quad (3)$$

The difference between the estimations of NEE or R_E by Equations 2 and 3 is caused by the functional change.

Partitioning of observed NEE and R_E to climatic variability versus functional change

When the functional change is detected with the HOS model, we partition variation of observed NEE or R_E values to four components, namely, the functional change, the direct effects of interannual climatic variability, the direct effects of seasonal climatic variation, and random error. This idea can be statistically realized by partitioning the sum of squares (SS) of the total deviation of all the data points from the mean (SS_T) as follows:

$$SS_T = SS_f + SS_{ic} + SS_{sc} + SS_e \quad (4)$$

where SS_f, SS_{ic}, SS_{sc} and SS_e are the sum of squares of deviation that can be explained by the functional change, interannual climatic variability, seasonal climatic variation, and random error, respectively. In this study, the SS for the functional change is calculated by:

$$SS_f = \sum_{i=1}^{y} \sum_{j=1}^{n} (\hat{Y}'_{ij} - \hat{Y}_{ij})^2 \quad (5)$$

where $\hat{Y}_{ij}$ and $\hat{Y}'_{ij}$ are the estimated NEE or R_E from Equations 2 and 3, respectively. The SS for the random error is estimated by:

$$SS_e = \sum_{i=1}^{y} \sum_{j=1}^{n} (Y_{ij} - \hat{Y}'_{ij})^2 \quad (6)$$

To estimate the other two components, we need to consider annual cycles of NEE or R_E. The comparison of values in a given year with the values at a similar point in the annual cycle in other years gives a measure of temporal variability within an ecosystem (Teal and Howes 1996). To calculate the variation among years caused solely by the climatic variables, we compared estimations of NEE or R_E from a multiple regression model (Equation 2) at a point in the annual cycle with the estimates from other years. These differences were caused solely by interannual climatic variability. The differences between mean values of estimated NEE or R_E across all years and the mean of all the estimated NEE or R_E values were caused by day-to-day changes in climatic variables. Mathematically, we expand $\hat{Y}_{ij}$ to linear components as:

$$\hat{Y}_{ij} = \overline{Y} + (\overline{Y}_{ij} - \overline{Y}_{.j}) + (\overline{Y}_{.j} - \overline{Y}) \quad (7)$$

where $\overline{Y}$ is the mean of all the estimated NEE or R_E values, and $\overline{Y}_{.j}$ is the mean of estimated NEE or R_E values from Equation 2 across all the years on the jth day. The terms $(\overline{Y}_{ij} - \overline{Y}_{.j})$ and $(\overline{Y}_{.j} - \overline{Y})$ represent interannual and seasonal deviations, respectively. Based on the linear components of NEE or R_E in Equation 7, we can estimate SS_{ic} and SS_{sc}, respectively, by:

$$SS_{ic} = \sum_{i=1}^{y} \sum_{j=1}^{n} (\hat{Y}_{ij} - \overline{Y}_{.j})^2 \quad (8)$$

$$SS_{sc} = \sum_{i=1}^{y} \sum_{j=1}^{n} (\overline{Y}_{.j} - \overline{Y})^2 \quad (9)$$

Division of SS_f, SS_{ic}, SS_{sc} and SS_e by SS_T results in the estimated contributions of the four components to observed variation in NEE or R_E.

If the functional change is determined to be not significant by the HOS model, we partition the variation of observed NEE or R_E values to three components, namely, the direct effects of interannual climatic variability, seasonal climatic variation and random error with Equations 6–9.

Analytical procedure

The analysis is divided into four steps.

Step 1: Simple regression of NEE and R_E on climatic variables We conducted simple regression analysis to examine whether a linear model can adequately describe variation of NEE and R_E against all the climatic variables. Among all the pairs of NEE and R_E against the climatic variables, only the relationship between R_E and temperature was marginally better described by a nonlinear equation than by a linear equation. Therefore, we used linear equations for the HOS analysis.

Step 2: Identification of significant climatic variables We performed a stepwise multiple regression analysis of NEE or R_E with climatic variables for data from all the years. All the climatic variables that were significantly correlated with NEE or R_E were included in the HOS analysis. The other variables were excluded from the analysis.

Step 3: Homogeneity-of-slopes analysis of NEE or R_E The HOS model considers year as a category variable that interacts with the climatic variables, resulting in the total number of variables equaling twice the number of climatic variables. We then examined whether all variables in the HOS model were significantly correlated with NEE or R_E. The stepwise procedure was applied iteratively to exclude insignificant variables until all variables were statistically correlated with NEE or R_E in the final model. If at least one of the slopes b_{ik} in Equation 1 was significantly different from zero, we inferred that functional change was statistically significant and climatic variability induced indirect effects on IAV in NEE or R_E. We then constructed a separate-slopes model.

Step 4: Partitioning of variation in NEE and R_E to climatic variability versus functional change We used Equation 4 to partition the total variability in observed NEE or R_E into four (if functional change exists) or three (if no functional change is detected) components as outlined previously. The statistical analyses were performed with SAS software (SAS Institute, Cary, NC).

Results and discussion

Ecosystem respiration, net ecosystem CO_2 exchange and climatic variables

Both observed R_E and NEE showed strong seasonal and interannual variations (Figure 1). In each year, R_E was low in winter and spring and gradually increased to maximum values in summer. Mean R_E in 1999 was the lowest among the five years (Table 1). In 2001, the mean value of R_E was 0.119 mg CO_2 m^{-2} s^{-1}, which was 83% higher than in 1999. Daily values of NEE also displayed clear seasonal variation, being nearly –5 g CO_2 m^{-2} day^{-1} in winter and about 25 g CO_2 m^{-2} day^{-1} in summer (Figure 1b). Observed NEE also showed considerable year-to-year variation. Annual means of NEE ranged from 6.70 g CO_2 m^{-2} day^{-1} in 1997 to 11.14 g CO_2 m^{-2} day^{-1} in 2001 (Table 2).

Climatic variables such as daily mean IPAR, T_A and T_S (data not shown, but similar to T_A) showed strong seasonal variations, whereas W_S, VPD and WS displayed weak seasonal

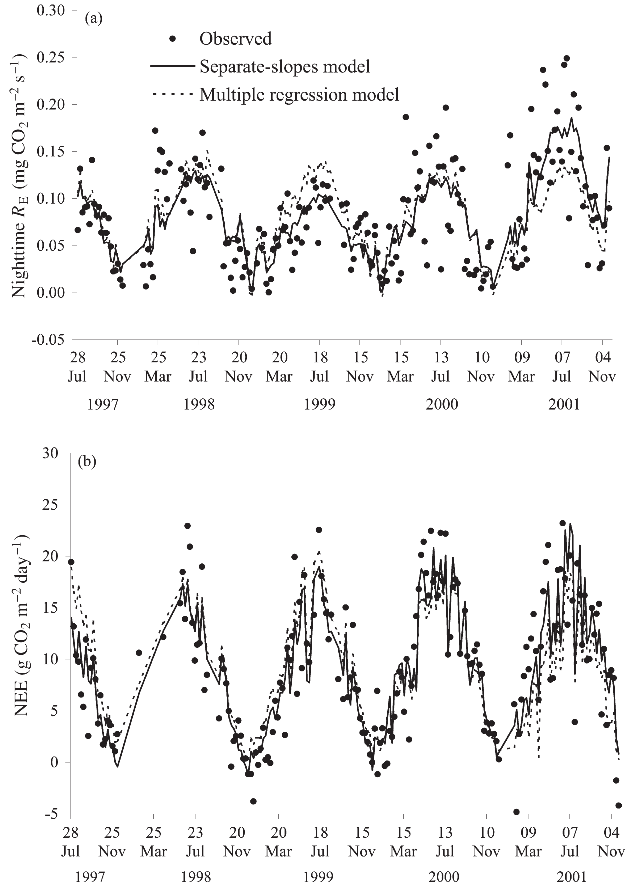

Figure 1. Nighttime ecosystem respiration (R_E) (a) and net ecosystem exchange of CO_2 (NEE) (b) measured in the Duke Forest from August 1997 to December 2001. Dashed line denotes estimates of the multiple regression model: $R_E = -0.00384 + 0.0055T_A + 0.0205\text{WS}$, $R^2 = 0.44$; and NEE = –0.8717 + 0.6038IPAR – 2.1305WS – 4.2323VPD, $R^2 = 0.69$. Solid line denotes estimations of the separate-slopes model: $R_E = 0.0181 + 0.0049T_A$ (if year = 1997) + $0.0048T_A$ (if year = 1998) + $0.0038T_A$ (if year = 1999) + $0.0048T_A$ (if year = 2000) + $0.0076T_A$ (if year = 2001), $R^2 = 0.56$; and NEE = –1.1096 + 0.5985IPAR – 2.7750WS – 8.0418VPD (if year = 1997) – 3.6212VPD (if year = 1998) – 4.8358VPD (if year = 1999) – 0.4793VPD (if year = 2000) + 2.7973VPD (if year = 2001), $R^2 = 0.79$.

Table 1. Mean values of nighttime R_E and the climatic variables (M_S = soil water content; P_D = ecosystem CO_2 exchange; T_A = air temperature; T_S = soil temperature). Data used in 1997 are from August 1997 to December 1997. The mean values were obtained by averaging half-hourly data from 2030 to 0430 h over 7 days. Sample size is the number of mean values in one year.

Variable	1997	1998	1999	2000	2001
Sample size (n)	20	39	45	49	44
R_E (mg CO_2 m^{-2} s^{-1})	0.069	0.079	0.065	0.072	0.119
T_A (°C)	10.5	12.8	11.9	11.6	13.4
T_S (°C)	14.8	14.6	14.4	14.6	15.7
M_S (volumes)	0.252	0.262	0.315	0.324	0.277
P_D (mg CO_2 m^{-2} s^{-1})	0.308	0.307	0.317	0.387	0.490
WS (m s^{-1})	0.949	0.947	0.954	0.815	0.990

Table 2. Mean values of NEE and climatic variables (IPAR = intercepted photosynthetically active radiation; M_S = soil water content; RH = relative humidity; T_A = air temperature; T_S = soil temperature; VPD = vapor pressure deficit; and WS = wind speed) in each year. Data used in 1997 are from August 1997 to December 1997. Sample size is the number of mean values (i.e., daily values averaged over one week) in one year.

Variable	1997	1998	1999	2000	2001
Sample size (n)	20	27	48	50	44
NEE (g CO_2 m^{-2} day^{-1})	6.70	8.96	7.54	10.10	11.13
IPAR (mol m^{-2} day^{-1})	25.44	26.55	24.82	23.72	24.13
T_A (°C)	16.8	17.6	14.2	14.3	16.3
T_S (°C)	15.2	16.4	13.9	14.4	15.5
M_S (volumes)	0.248	0.226	0.321	0.319	0.276
VPD (kPa)	0.551	0.720	0.591	0.478	0.544
RH	0.769	0.737	0.710	0.754	0.751
WS (m s^{-1})	1.15	1.17	1.18	0.99	1.31

trends but large day-to-day variations (Figure 2). Yearly mean values of climatic variables differed among the years. For example, yearly mean nighttime T_A ranged from 10.5 °C in 1999 to 13.4 °C in 2001 (Table 1). Yearly means of daily values in T_A ranged from 17.6 °C in 1998 to 14.2 °C in 1999 (Table 2).

Relationships between nighttime R_E and climatic variables

Simple regression analysis was conducted on nighttime R_E with the climatic variables (Figure 3). Among the climatic variables, T_A had the largest influence on R_E, and T_S also significantly influenced R_E. Based on mean daily data, the linear regression equations of R_E with temperatures were adequate because the commonly used exponential equation only slightly improved the fitting (coefficient of determination r^2 increased from 0.43 to 0.45 and 0.35 to 0.37 for T_A and T_S, respectively). The linear relationship was also found suitable at a subarctic fen (Griffis et al. 2000). Soil water content had a weak negative influence on R_E (Figure 3c), P_D had a significant influence on R_E (Figure 3d), and WS did not influence R_E significantly (Figure 3e).

Climatic variables were significantly correlated with each other. For example, high T_A was always correlated with high T_S (r_{T_A,T_S} = 0.94), low M_S (r_{T_A,M_S} = –0.52), and high P_D (r_{T_A,P_D} = 0.82) in the Duke Forest. To consider the correlations among climatic variables, we conducted a multiple regression analysis of nighttime R_E with WS, T_A, T_S, M_S and P_D. A stepwise method was used to select climatic variables with entry and elimination probabilities of 0.05. Several iterations of the stepwise regression analysis yielded the best regression equation, $R_E = -0.0038 + 0.02046\text{WS} + 0.0055T_A$, with a coefficient of determination R^2 = 0.44. Path analysis revealed that T_A was more important (path coefficient p_{T_A} = 0.69) than WS (p_{WS} = 0.12).

Although the best regression equation generally fit the measurement data well, a large portion of variation in R_E (56%) could not be explained by these variables (Figure 4a). Eddy-covariance measurements of nighttime CO_2 fluxes are sensi-

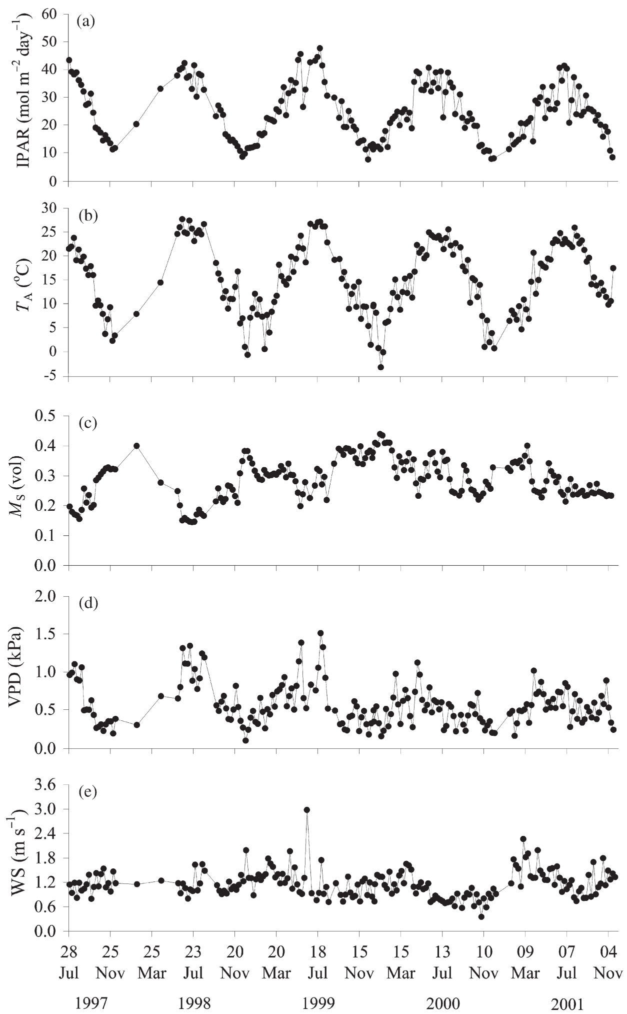

Figure 2. Change in climatic variables in the Duke Forest from August 1997 to December 2001. Abbreviations: IPAR = intercepted photosynthetically active radiation; M_S = soil water content; T_A = air temperature; VPD = vapor pressure deficit; and WS = wind speed.

tive to the intermittency and spatial variability (within the footprint) of forest floor fluxes; hence it is not surprising that the "random noise" is large. Furthermore, the biophysical processes regulating ecosystem respiration are complex and may be plagued by high spatial variability attributed to spatial (rather than temporal) variability in soil water content and litter. There is a need to identify ecological mechanisms underlying the variability in R_E and NEE, as well as to improve nighttime measurement accuracy of the eddy-covariance flux technique (Lee 1997).

Interannual variability and seasonal variation of nighttime R_E

Multiple regression analysis showed that WS and T_A significantly influenced nighttime R_E. We applied an HOS model to detect if the slopes of WS and T_A varied among years. We found that the interaction between T_A and year was significant. After considering this interaction, the effect of WS on R_E be-

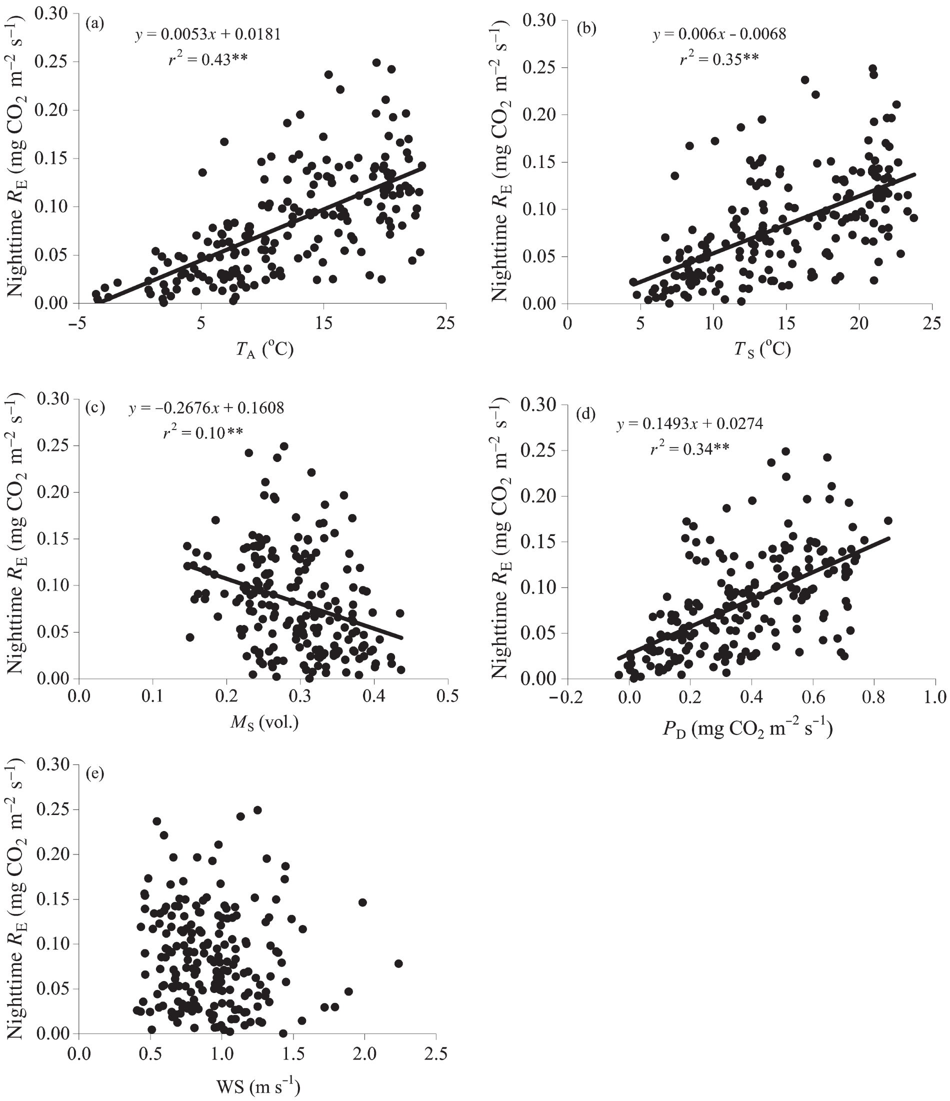

Figure 3. Relationships between nighttime R_E and the climatic variables (M_S = soil water content; P_D = ecosystem CO_2 exchange; T_A = air temperature; T_S = soil temperature; and WS = wind speed). Double asterisks denote significance at the 0.01 level.

came insignificant and was excluded from the model. The final HOS model included T_A and its interaction with year (Table 3) and indicated that the functional relationship of R_E with temperature varied among years. Because IAV in R_E was partially caused by the functional change in ecosystem processes, we fitted the data using a separate-slopes model (Equation 3). As a result, the estimation of R_E was markedly improved (Figures 1a and 4a), with R^2 increasing from 0.44 to 0.56.

The detected functional change that contributed to IAV in R_E is consistent with results from other studies. For example, long-term exposure of ecosystems to different temperature regimes usually results in adjustments in temperature sensitivity of soil respiration (e.g., Kirschbaum 1995, Luo et al. 2001). The adjustments in temperature sensitivity of ecosystem respiration may be related to changes in substrate quantity and quality, microbial community structure, and plant productivity (Luo et al. 2001). Savage and Davidson (2001) also found that parameter values of a regression model linking soil respiration with soil temperature varied among years in upland sites at the Harvard Forest, MA. They concluded that temperature functions predicted seasonal variation in soil respiration well and suggested that interactive effects of temperature with precipitation and soil water content may complicate our understanding of interannual variability in soil respiration. Nonetheless, our statistical analysis attributed the observed total variation in R_E to four components: 13.1% caused by functional change, 5.0% by interannual climatic variability, 38.1% by seasonal climatic variation and 43.8% by random error.

Relationships between NEE and climatic variables

The NEE of a forest ecosystem varies with environmental driving forces, such as radiation, temperature, and their effects on ecological processes (Melillo et al. 1993, Peng et al. 1995, Baldocchi and Meyers 1998). In this study, NEE was linearly correlated with daily total IPAR (Figure 5a). Nonlinear relationships of ecosystem CO_2 flux with light are often observed in half-hourly measurements (Clark et al. 1999, Luo et al. 2000, Chen et al. 2002). When daily totals are calculated, however, linear functions are usually adequate to correlate NEE with IPAR (Leuning et al. 1995). Ruimy et al. (1995) compiled

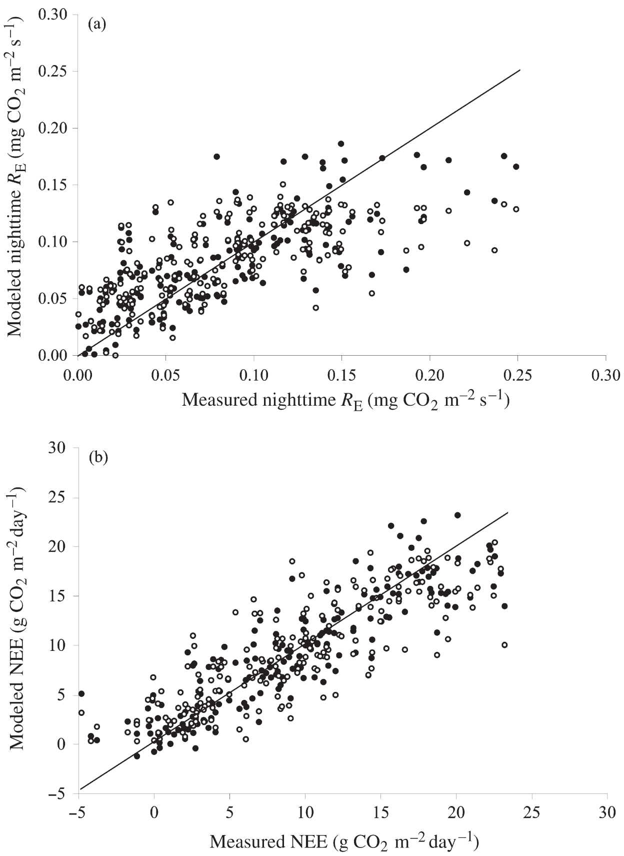

Figure 4. Comparison of model estimations and measurements of nighttime ecosystem respiration (R_E) (a) and net ecosystem exchange of carbon (NEE) (b). Symbols: ○ = values estimated by the multiple regression model; and ● = values estimated by the separate-slopes model.

published data on daily integrated canopy CO_2 flux in relation to daily radiation and concluded that the relationship is approximately linear for all vegetation types and under all environmental conditions.

The NEE was linearly correlated with T_A and T_S based on daily values (Figures 5b and 5c), whereas VPD, M_S, RH and WS showed weak linear correlations with NEE (Figures 5d–5g). Similar to IPAR, the nonlinear relationships of ecosystem photosynthesis and VPD, M_S, RH and T_A appear for half-hourly data, but linear equations describe the relationships well for the daily data. The positive effect of VPD on NEE and the negative effect of M_S on NEE could not be easily explained. Because VPD was high in summer and low in winter, and M_S was high in winter and low in summer in the Duke Forest, the observed relationships may reflect correlations and interactions among climatic variables themselves.

We found significant correlations between mean daily T_A and T_S (r = 0.93), between IPAR and T_A (r = 0.83), and between IPAR and T_S (r = 0.78). The IPAR had a relatively small negative influence on M_S (r = –0.44), and M_S showed negative correlations with all other climatic variables, and strongly correlated with T_S (r = –0.54), VPD (r = –0.53), and T_A (r = –0.52). Wind speed was weakly correlated with RH, T_S and T_A. The interactions among climatic variables necessitated multiple regression analysis.

The multiple regression analysis of NEE against climatic variables showed that IPAR, VPD and WS significantly influenced NEE: NEE = –0.8717 + 0.6038IPAR – 4.2323VPD – 2.1305WS, R^2 = 0.69. Path analysis indicated that IPAR is the most important factor (path coefficient p = 0.93). Both WS and VPD had a small negative influence on NEE (p = –0.11 and –0.18 for WS and VPD, respectively) compared with IPAR. Similar results were obtained for Douglas-fir stands based on eddy-covariance measurements (Chen et al. 2002), with NEE strongly correlated with PAR and VPD. This relationship was also found at the leaf level, with photosynthesis usually responding negatively to increasing VPD (Day 2000). However, Morecroft and Roberts (1999) found no relationship between photosynthesis and VPD mainly because stimulation of photosynthesis by high PAR overcompensated for the reduction by VPD. Myers et al. (1999) reported that T_A is a primary influence on the photosynthetic responses of loblolly pine trees in the Duke FACE experiment. We found no significant effect of T_A or T_S on NEE. This may be associated with the significant correlation of IPAR and T_A and T_S. In the Duke Forest, NEE was also not limited by soil water availability, except during severe drought periods.

Interannual variability and seasonal change of NEE

The HOS analysis indicated that the effect of VPD on NEE varied among years, whereas the effects of IPAR and WS on NEE did not change among years (Table 4, Figure 1b). Because functional change was detected in NEE, we constructed a separate-slopes model. Compared with the multiple regression model, the separate-slopes model improved the NEE estimation substantially, with R^2 increasing from 0.69 with the multiple regression model to 0.79 with the separate-slopes model (Figure 4b). The separate-slopes model accounted for 9.9% more variation in observed NEE than the multiple regression model, which is attributed to the functional change. The other 90.1% variation in observed NEE was partitioned to interannual climatic variability (8.9%), seasonal climatic variation (59.9%), and random error (21.3%). The partitioning of variation indicated that the functional change accounts for more IAV in NEE than the year-to-year changes in climatic variability. Braswell et al. (1997) also suggested greater indirect effects than direct effects of climatic variability on NEE

Table 3. An ANOVA of a homogeneity-of-slopes model of ecosystem respiration (R_E). Double asterisks denote significant differences among variables at the 0.01 level.

Source	df	SS	MS	F
Homogeneity-of-slopes model	5	0.3217	0.0643	48.98**
T_A	1	0.2463	0.2463	187.53**
T_A × Year	4	0.0754	0.0188	14.35**
Error	191	0.2509	0.0013	
Total	196	0.5726		

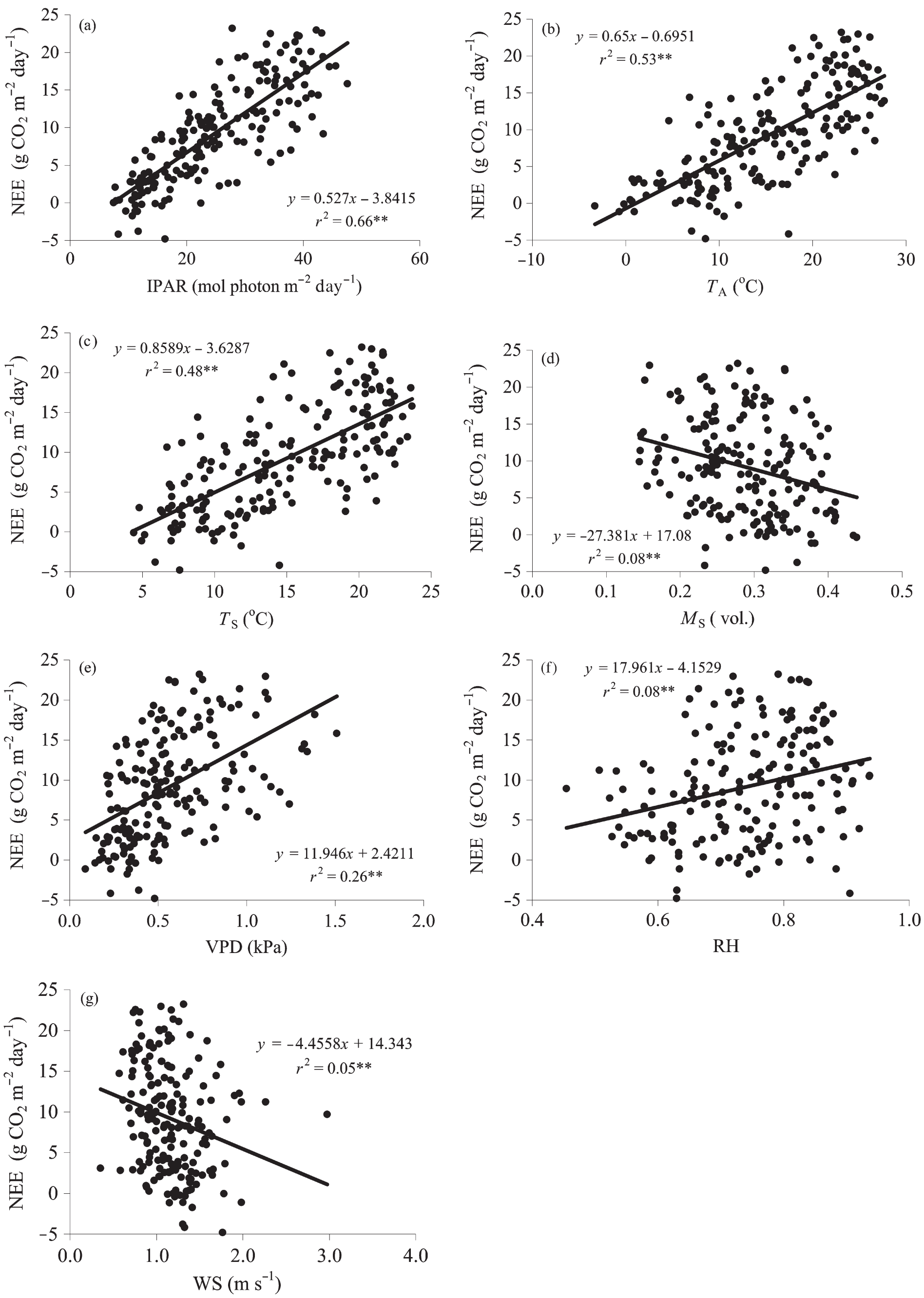

Figure 5. Relationships between net ecosystem CO_2 exchange (NEE) and the climatic variables IPAR (intercepted photosynthetically active radiation), M_S (soil water content), RH (relative humidity), T_A (air temperature), T_S (soil temperature), VPD (vapor pressure deficit) and WS (wind speed). Double asterisks denote significance at the 0.01 level.

Table 4. An ANOVA of a homogeneity-of-slopes model of NEE and climatic variables. Double asterisks denote significant differences among variables at the 0.01 level.

Source	df	SS	MS	F
Homogeneity-of-slopes model	7	6353.69	907.70	95.32**
WS	1	136.18	136.18	14.30**
IPAR	1	5306.35	5306.35	557.24**
VPD	1	114.33	114.33	12.01**
VPD × Year	4	796.83	199.21	20.92**
Error	181	1723.57	9.52	
Total	188	8077.25		

based on the finding of substantial lagged responses of NDVI and growth rate to atmospheric CO_2 concentration and temperature. When both the direct effect of climatic variability and the functional change on NEE exist, short-term observations often cannot provide enough information to establish reliable predictive relationships with climatic variables. Thus, interpretation of IAV in R_E and NEE that is mainly caused by functional change requires long-term measurements.

Conclusions and implications

We proposed a framework for detecting and partitioning IAV in NEE using multi-year eddy flux measurements collected at the Duke pine forest. We used an HOS model to detect the functional change in ecosystem processes that contributed considerably to IAV in NEE and R_E. With a combination of the separate-slopes model and the multiple regression model, we partitioned IAV in NEE and R_E into four components, namely, functional change, climatic variability among years, seasonal variation and random error. We found that 13.1% of variation in observed R_E was explained by functional change, 5.0% by interannual climatic variability, and nearly 38.1% by seasonal variation in climatic variables. Nearly 10% of the variation in observed NEE was explained by functional change, 8.9% by interannual climatic variability, and 59.9% by seasonal variation in climatic variables.

To our knowledge, this is the first report of the use of statistical analysis to separate the different sources of interannual variability. We demonstrated that it is feasible to partition the variation in ecosystem carbon fluxes into direct effects of seasonal and interannual climatic variability, and indirect effects or functional change. Although our linear model may not be directly applicable to other conditions, the principle can be applied in similar studies.

Understanding the causes and degree of IAV in ecosystem carbon fluxes is important for both development of ecological theories and projections of future ecosystem changes. If IAV is not significant, as is the case for productivity of frequently flooded salt-marsh areas (Teal and Howes 1996), measurements made in any single year can be applied to other years with suitable precautions to account for seasonal cycles. If IAV in NEE exists and is caused purely by direct effects of climatic variability, we cannot extrapolate measurements from one year to another year. However, the relationship, either linear as demonstrated in this study, or some nonlinear form derived from short-term measurements, can be used to project long-term changes as long as we have realistic future climate scenarios. If the climate-induced functional change in ecosystem processes contributes significantly to IAV in ecosystem carbon fluxes, long-term observations are required to develop a sound understanding of the relationships between NEE and climatic variables before we can reasonably predict ecosystem carbon fluxes. Under this circumstance, current ecological models often successfully simulate NEE in some years but fail in others (e.g., Griffis and Rouse 2001). Statistical models that consider only the correlation of NEE with climatic variables are also unable to reproduce realistic interannual variation, because of their inability to capture functional change (Goward and Prince 1995, Goetz et al. 2000). Process-based models are useful for predicting IAV in NEE only if the functional change caused by the indirect effect of climatic variables is appropriately incorporated into the model (Goetz et al. 2000, Knorr 2000). The broader implication of this study is that the next generation of mechanistic models must be able to deal with functional change if progress is to be made on estimating carbon cycling at annual and longer time scales.

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