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A nonparametric method for separating photosynthesis and respiration components in CO_2 flux measurements

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[1] Future climate change is expected to affect ecosystem-atmosphere CO_2 exchange, particularly through the influence of temperature. To date, however, few studies have shown that differences in the response of net ecosystem CO_2 exchange (NEE) to temperature among ecosystems can be explained by differences in the photosynthetic and respiratory processes that compose NEE. Using a new nonparametric statistical model, we analyzed data from four forest ecosystems. We observed that differences among forests in their ability to assimilate CO_2 as a function of temperature were attributable to consistent differences in the temperature dependence of photosynthesis and respiration. This observation provides empirical validation of efforts to develop models of NEE from the first-principle relationships between photosynthetic and respiratory processes and climate. Our results also showed that models of seasonal dynamics in NEE that lack specific consideration of the temperature dependence of respiration and photosynthesis are likely to carry significant uncertainties. *INDEX TERMS:* 0315 Atmospheric Composition and Structure: Biosphere/atmosphere interactions; 1615 Global Change: Biogeochemical processes (4805); 3307 Meteorology and Atmospheric Dynamics: Boundary layer processes; 3322 Meteorology and Atmospheric Dynamics: Land/atmosphere interactions; 4806 Oceanography: Biological and Chemical: Carbon cycling. **Citation:** Yi, C., et al. (2004), A nonparametric method for separating photosynthesis and respiration components in CO_2 flux measurements, *Geophys. Res. Lett.*, *31*, L17107, doi:10.1029/2004GL020490.

1. Introduction

[2] Carbon exchanges between the global biosphere and the atmosphere are critical to determining the CO_2 concentration of the atmosphere and its coupled influence on the Earth's climate. Net ecosystem CO_2 exchange (NEE) reflects the balance between two large CO_2 fluxes, gross photosynthesis and ecosystem respiration (R_e), and is currently being measured at over 200 sites worldwide as part of regional CO_2 flux networks [*Baldocchi et al.*, 2001]. NEE is typically measured with the eddy covariance method, which provides a direct measurement of the turbulent CO_2 flux above the canopy. However, eddy covariance provides a net flux, and seasonal or interannual dynamics in NEE cannot be adequately explained without a means to partition the net flux into its component gross fluxes.

[3] A common model used to gain insight into the component fluxes of NEE can be stated as:

$$F = R_e - \alpha Q F_\infty / (\alpha Q + F_\infty), \qquad (1)$$

where F is NEE, Q is the photosynthetic photon flux density, R_e is the ecosystem respiration rate, F_∞ is the light-saturated net ecosystem CO_2 flux, and α is the light-use efficiency of NEE (or apparent quantum yield). It is not possible to obtain a true gross ecosystem CO_2 exchange flux from equation (1), but it is possible to use equation (1) to partition NEE into low light regimes where effects on R_e exert primary influences on NEE and high light regimes where effects on photosynthesis exert primary influences on NEE. This model has been used in a number of past studies to analyze the response of NEE to light intensity, and to partition NEE into its component processes [e.g., *Wofsy et al.*, 1993; *Ruimy et al.*, 1995; *Barcza*, 2001]. In these studies, it is usually assumed that the daytime ecosystem respiration is an exponential function of temperature, $R_e = Ae^{BT}$, where A and B can be estimated by nighttime NEE and temperature measurements. However, some apparent uncertainties associated with this approach are: (1) Nighttime NEE can not be accurately measured by the eddy covariance technique especially during calm nights [*Goulden et al.*, 1996; *Yi et al.*, 2000]; (2) Daytime R_e is different from nighttime R_e because of light-induced inhibition of leaf respiration [*Brooks and Farquhar*, 1985]; (3) Daytime R_e may not have the expected exponential relationship with temperature [*Tjoelker et al.*, 2001].

[4] We developed a new nonparametric statistical method that allowed us to use equation (1) in an inverse mode; we constrain the relationship between F and Q using data from the four forest sites, and then use a nonparametric regression approach to obtain optimized estimates of the parameters in

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equation (1) (R_e, F_∞ and α). This new nonparametric statistical method provides an independent way to investigate the temperature dependence of components of NEE. The results of our study provide the insight needed to improve representation of the effect of temperature on NEE in regional and global carbon budget models.

2. Material and Methods

2.1. Study Sites and Data Acquisition

[5] This study was carried out at four forest sites within the AmeriFlux network [*Baldocchi et al.*, 2001]: the WLEF tall-tower site in northern Wisconsin (45.95°N, 90.27°W, hereafter referred to as WL); the Niwot Ridge site in the Rocky Mountains of central Colorado (40.03°N, 105.05°W, NWR); the Walker Branch Watershed Site in eastern Tennessee (35.96°N, 84.29°W, WB); and the Harvard Forest Environmental Measurement Site in central Massachusetts (42.52°N, 72.18°W, HV).

[6] The WL site is in a region of cold temperate mixed forest with abundant wetlands. The dominant forest types are mixed northern hardwoods, aspen, pine, and forested wetlands [*Yi et al.*, 2000]. The NWR site is in a subalpine forest at approximately 3050 m elevation above sea level. The forest has regenerated following clear-cut logging in the early 1900s, and it consists primarily of lodge pole pine, Engelmann spruce, and subalpine fir [*Monson et al.*, 2002]. The WB site is located in the southern section of the temperate deciduous forest biome in the eastern United States. The predominant species in the forest stand include oak, maple, tulip poplar and loblolly pine [*Wilson et al.*, 2001]. The HV site is located in a mixed temperate forest that includes hardwood and conifer species. The forest stand is approximately 70 years old, and is dominated by red oak and red maple. [*Goulden et al.*, 1996].

[7] Measurements of NEE at each site were made according to the eddy flux technique [*Massman and Lee*, 2002]. Data for this study were obtained as half-hour flux and microclimate averages from the Fluxnet database at Oak Ridge National Laboratory's Data Archive and Analysis Center. The data we used are in daytime of growing season (June through August) and include the NEE, Q, and air temperature. The reason for using the growing season data is that the leaf area index in summer (June through August) is almost constant relative to spring and autumn. The gap-filled data were excluded. The years of data for each site are as follows: WB (1995–1998); HV (1992–1999); WL (1997–2001); and NWR (1999–2002).

2.2. Data Analysis

[8] In order to obtain a robust analysis of NEE as it responds to variable temperature and light we analyzed data from each site collected across the full growing season. Our approach was to isolate the relationship between F and Q according to equation (1); in statistical terms equation (1) reflects a regression analysis with the accompanying theoretical constraint that all parameters on the right-hand side must be constant except the independent variable (in this case, Q). In reality, R_e, F_∞ and α vary with temperature and other climatic conditions (e.g., soil and atmospheric moisture content), such that data obtained from the entire growing season cannot ideally satisfy the theoretical statistical constraints. In order to use equation (1) in a relaxed form, we applied the equation separately to three different temperature regimes represented in each growing season data set; low, medium and high. To choose these three regimes, we sorted the seasonal data for each site into a 20% bin with the lowest temperatures, a 20% bin with the highest temperatures, and a 60% bin with intermediate temperatures. Constant values for R_e, F_∞ and α were calculated as the mean for each temperature bin and applied to equation (1). This approach allowed us to obtain response curves for F versus Q at three different temperature regimes for each site, and thus assess the degree to which the light-dependence of NEE was sensitive to temperature. This approach can be described as the forward projection of equation (1), and hereafter is referred to as FM (forward projection model).

[9] In order to take the analysis a step further, and obtain information on the temperature dependence of the respiratory and photosynthetic components of NEE, we used equation (1) in an inverse projection; constraining the model with data for F and Q, while developing a nonparametric statistical model to solve for the temperature dependence of R_e, F_∞ and α. We begin with the hypothesis that R_e, F_∞ and α are functions of temperature and rewrite equation (1) as:

$$\begin{aligned} F(T,Q) &= R_e(T) - \alpha(T)QF_\infty(T)/(\alpha(T)Q + F_\infty) \\ &= f\{Q;\beta(T)\} + \delta, \end{aligned} \tag{2}$$

where δ is the mean zero random error, and $f\{Q;\ \beta(T)\}$ is a nonlinear function of Q, and each component ($R_e(T)$, $F_\infty(T)$, $\alpha(T)$) of $\beta(T)$ that are smoothing functions of T. In statistical terms, equation (2) is called a nonlinear varying coefficient model. We used a nonparametric statistical method to estimate functions $\beta(T)$. One of the advantages of this method is that there is no requirement to impose an assumption on the functional form of $\beta(T)$. The Newton-Raphson algorithm was employed in searching for functions of $\beta(T)$. The details about the nonlinear varying coefficient model can be found in the auxiliary material[1] and *Cai et al.* [2000]. Hereafter we will refer to equation (2) as an inverse projection model (IM).

3. Results and Discussion

[10] The forests at the WB and NWR sites exhibited significant reductions in NEE at all values of Q as temperature increased (Figures 1a and 1d). The forest of the WL site exhibited little response in NEE to increases in seasonal temperature (Figure 1c). The forest of the HV site exhibited a slight increase in F at moderate-to-high values of Q as seasonal temperature increased (Figure 1b). Although the southeastern deciduous forest of WB and the subalpine coniferous forest of NWR exhibited similarity in the negative responses of NEE to increased temperature, they also exhibited one sharp difference that likely has ecological relevance. The forest of WB exhibited a much higher ratio of F_∞ to R_e at all temperatures, compared to the forest of NWR ($F_\infty/R_e \approx 17$ for the forest at WB and $F_\infty/R_e \approx 2$ for the forest at NWR at 20°C). This difference

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[1] Auxiliary material is available at ftp://ftp.agu.org/apend/gl/2004GL020490.

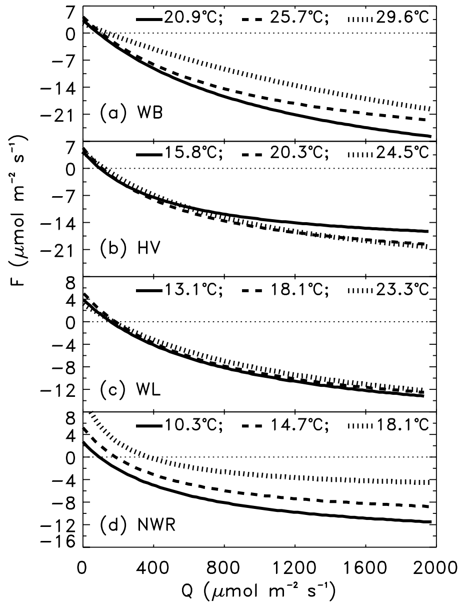

Figure 1. Ecosystem light response curves for each AmeriFlux site for three different temperature regimes. The regression curves were obtained by fitting the data using equation (1). More negative numbers mean greater carbon uptake from atmosphere by ecosystems.

is due to a slightly lower R_e for the NWR forest compared to the WB forest, but a substantially lower F_∞, reflecting the greater inherent photosynthetic constraints of the subalpine coniferous forest.

[11] The forest at HV exhibited a slight increase in F at high Q and high temperature, in contrast to the forests at WB and NWR (Figure 1). The trend for the HV forest is due to increases in F_∞ as temperature increases which, because of its much higher value compared to R_e, more than offsets the negative effect of increasing of R_e at high temperature (Figure 2). F_∞ increasing with seasonal temperature in the HV forest may be related to inhibition of gross photosynthesis at cool temperatures. This hypothesis is supported by the leaf-level photosynthesis measurements conducted at the HV forest by *Bassow and Bazzaz* [1998]. In fact, compared to the WB forest, F_∞ is lower at all temperatures in the HV forest, but this difference is especially pronounced at the lowest temperature range (Figure 2b). These contrasting trends are consistent with past observations of seasonality in leaf-level measurements of net photosynthesis rate. *Wilson et al.* [2001] observed a distinct early season peak in F_∞, followed by mid-summer declines in the dominant trees of the WB forest. This pattern was attributed to leaf age effects on the maximum photosynthetic carboxylation capacity of the leaf (V_{cmax}), perhaps due to declines in leaf Rubisco activity. In contrast, in the dominant trees of the HV forest, *Bassow and Bazzaz* [1998] observed an increase in leaf-F_∞ from the early part of the growing season (June) to the middle of the growing season (July); late-summer net photosynthesis rates dropped again. From these leaf-level observations, one would predict a decrease and increase in F_∞ as the growing season progresses for the WB and HV forests, respectively; similar to what we observed.

[12] The decrease in R_e as temperature increases at the WL site (Figure 2a) is not normally observed in observations of ecosystem respiration, unless water stress covaries with warm temperature [*Davidson et al.*, 1998]. We examined the data set for the WL site more closely and determined that observations for the highest temperature bin, when applied to equation (1), occurred almost exclusively at Q values greater than 2000 μmol m^{-2} s^{-1} and at atmospheric vapor pressure deficits greater than 2 kPa (Figure 3a). In contrast, data in the lowest temperature bin occurred at lower values for Q (almost exclusively below 1000 μmol m^{-2} s^{-1}, and with most of the data occurring below 600 μmol m^{-2} s^{-1}) and lower values for VPD. The observations for the middle-temperature bin were evenly distributed between the extremes of the high- and low-temperature bins. This bias in the distribution of the data causes equation (1) to predict a nearly linear trend for the high temperature bin (with concomitant significantly lower intercept, R_e), compared to data in the middle temperature bin; which in turn would cause an apparent decrease in the predicted R_e as temperature is increased (Figure 2). The available soil moisture data also provides evidence that the reduction in the ecosystem respiration R_e at higher temperature was caused by water stresses (Figure 3b).

[13] In deriving the temperature response of the photosynthetic and respiratory components of NEE, we used equation (1) in an inverse projection; we constrained the relationship between F and Q by assimilating data from the four sites, and then used a novel nonparametric approach to search for optimized estimates for the components of NEE at each respective temperature. We asked the question: Does the use of the inverse projection of equation (1), with

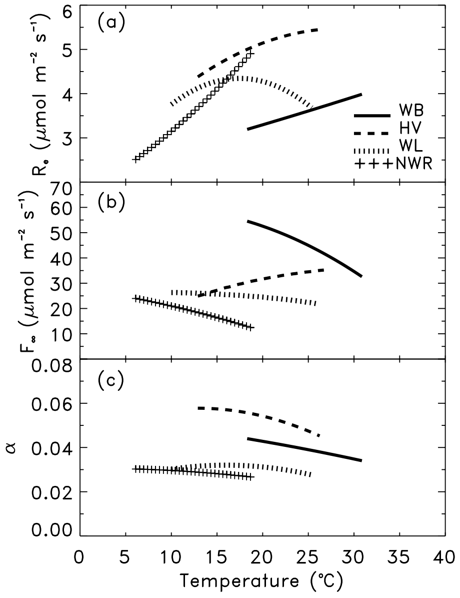

Figure 2. Relationships between light response parameters and temperature: (a) ecosystem respiration R_e; (b) ecosystem light-saturated net photosynthetic rate F_∞ and (c) ecosystem apparent quantum yield α. The data used were the same as in Figure 1. 5% of each curve in (a)–(c) at the ends of low and high temperature was trimmed to reduce the uncertainties associated with the statistical boundary effects.

parameterization of F_∞, R_e and α across the seasonal temperature gradient, provide results that are significantly different than those provided by the forward projection? Predictions of the F versus Q relationship using the IM deviated from those using the FM for forests at two of the sites (WB and NWR) (Figures 4a and 4d). The two approaches produced no significant differences for the forest at HV and WL (Figures 4b and 4c). For the NWR forest and WB forest, the FM approach resulted in a 38 and 13% overestimation of α, respectively, and a 22 and 24% underestimation of F_∞, respectively (see auxiliary material). The differences between these approaches at the NWR and WB sites are due to consideration of the seasonal temperature-dependencies of F_∞, R_e and α in the IM approach, but lack of such consideration in the FM approach. In the two ecosystems where NEE was most affected by temperature (WB and NWR), and in which the photosynthetic and respiratory components of NEE respond to temperature in opposite directions, the inability of the FM approach to account for temperature sensitivity causes error in the prediction. The lack of net temperature response in the parameters for the WL site, and the response to temperature in the same direction for R_e and F_∞ for the HV site, apparently preclude differences in the two modeling approaches. The nonparametric approach would appear to provide an improvement in the modeling of NEE and its component processes for those ecosystems in which seasonal temperature dependence is significant. The nonparametric approach may be especially useful as data from the various global CO_2 flux networks is analyzed for evidence of how forest carbon sequestration may respond to future climate change.

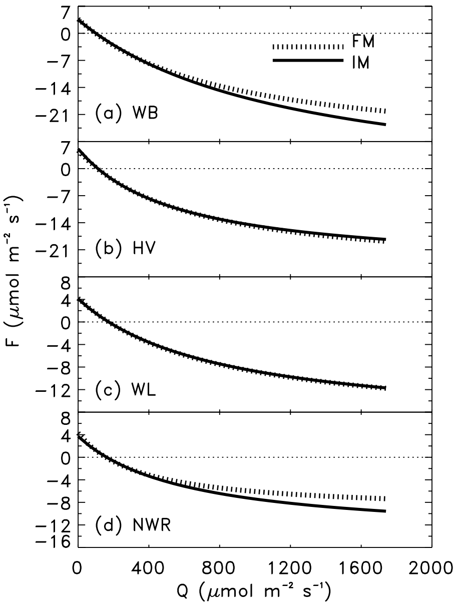

Figure 4. Comparison of ecosystem light response curves for each of the four forest sites using either the forward projection model (FM) or the inverse projection model (IM). The curve of the IM was obtained using the mean light response parameter values obtained from Figure 2.

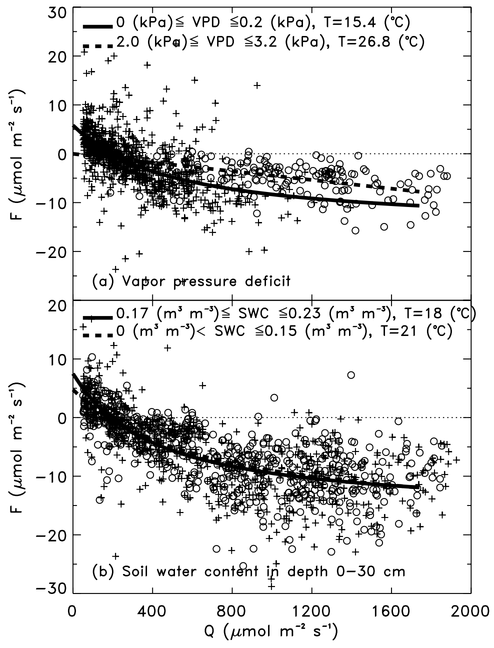

Figure 3. Comparison of ecosystem light responses at WL site under dryer (circle) and wetter (plus) conditions: (a) two extreme cases of VPD; (b) soil water content (SWC) in depth 0–30 cm. The values of temperature were the mean temperature of the subgroup data. The interception R_e in (a) is zero for the high VPD bin (dashed line) and 5.8 (μmol m^{-2} s^{-1}) for low VPD bin (solid line). The interception R_e in (b) is 4.8 (μmol m^{-2} s^{-1}) for dryer condition (dashed line) and 7.5 (μmol m^{-2} s^{-1}) for wetter condition (solid line).

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