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Climate control of terrestrial carbon exchange across biomes and continents

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Abstract

Understanding the relationships between climate and carbon exchange by terrestrial ecosystems is critical to predict future levels of atmospheric carbon dioxide because of the potential accelerating effects of positive climate–carbon cycle feedbacks. However, directly observed relationships between climate and terrestrial CO_2 exchange with the atmosphere across biomes and continents are lacking. Here we present data describing the relationships between net ecosystem exchange of carbon (NEE) and climate factors as measured using the eddy covariance method at 125 unique sites in various ecosystems over six continents with a total of 559 site-years. We find that NEE observed at eddy covariance sites is (1) a strong function of mean annual temperature at mid- and high-latitudes, (2) a strong function of dryness at mid- and low-latitudes, and (3) a function of both temperature and dryness around the mid-latitudinal belt (45°N). The sensitivity of NEE to mean annual temperature breaks down at ∼16 °C (a threshold value of mean annual temperature), above which no further increase of CO_2 uptake with temperature was observed and dryness influence overrules temperature influence.

Keywords: NEE, climate control, terrestrial carbon sequestration, temperature, dryness, eddy flux, biomes, photosynthesis, respiration, global carbon cycle

S Online supplementary data available from stacks.iop.org/ERL/5/034007/mmedia

1. Introduction

Determining the relationships between terrestrial carbon exchange and climate is fundamentally important because climate–carbon cycle feedback could significantly accelerate (or decelerate) future climate warming (Zeng *et al* 2004, 2005). Globally, the observed growth rate anomaly of atmospheric CO_2 concentration is correlated with the multivariate El Niño-Southern Oscillation index (Heimann and Reichstein 2008). Inversion modeling (Bousquet *et al* 2000) and biome-based analyses of climate anomalies (Zhou *et al* 2008) suggest that the oceanic carbon reservoir is a minor player in this variability. Instead, variations in the atmospheric CO_2 growth rate result largely from the impact of climate on terrestrial carbon sequestration (Nemani *et al* 2003, Xiao and Moody 2004), including regional impacts of extreme climate conditions such as heat waves and droughts (Ciais *et al* 2005, Xiao *et al* 2009).

On much smaller spatial scales, large amounts of data have been collected continuously over the last two decades using the eddy covariance technique to measure directly the net ecosystem exchange of CO_2 (NEE) between the biosphere and the atmosphere (Baldocchi *et al* 2001, Law *et al* 2002). Although a typical eddy covariance footprint is relatively small (ca. 1 km^2), NEE variability at these sites is often representative of variability over much larger spatial scales as a result of the spatial coherence of climate anomalies (Ciais *et al* 2005, Nemani *et al* 2003, Xiao and Moody 2004). These temporal variations in NEE, the imbalance between photosynthesis (fixation of atmospheric carbon dioxide into organic carbon) and ecosystem respiration (plant and microbial respiration converting organic carbon into atmospheric carbon dioxide), are caused predominately by climatic drivers on daily and seasonal timescales (Law *et al* 2002). Although several synthesis efforts have been conducted across eddy-flux tower sites, the role of climatic drivers in causing NEE variability across multiple sites on annual or longer timescales is still not clear (Law *et al* 2002, Valentini *et al* 2000, Reichstein *et al* 2007).

Determining the environmental controls on NEE is complicated because NEE is the difference between photosynthesis and ecosystem respiration, and climate variations may affect these two components in different ways. Spatial variability in respiration is strongly correlated with temperature, precipitation and substrate supply (Raich *et al* 2002, Ryan and Law 2005), and gross primary productivity has been shown to be subject to climate-based limiting factors—temperature, precipitation and/or radiation, depending on the region (Law *et al* 2002). This paper seeks to identify the climate controls on spatial NEE variability globally as represented within FLUXNET, a global network of eddy covariance tower sites (Baldocchi *et al* 2001). Other studies have shown that non-climate factors, especially disturbance, are a major factor causing NEE variability (Oren *et al* 2006, Thornton *et al* 2002, Foley *et al* 2005). The role of disturbance history may be underplayed in FLUXNET synthesis studies because the number of recently disturbed sites is limited. However, we expect that other recent estimates that emphasize the effects of other non-climate factors such as nitrogen (Magnani *et al* 2007, Sutton *et al* 2008) have downplayed the role of climatic interactions.

2. Data and sites

The present analysis is based on 559 site-years of eddy covariance data measured from 125 sites throughout the world from 1992 to 2008 (supplementary table S1 available at stacks.iop.org/ERL/5/034007/mmedia). The latitudes

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vary from 37°S to 71°N, longitudes are broadly covered, and elevation ranges from −2 to 3288 m (supplementary figure S1 available at stacks.iop.org/ERL/5/034007/mmedia). The climatic zones of the sites include polar tundra, maritime temperate, continental temperate, humid subtropical, Mediterranean, arid, semi-arid, tropical monsoon, and tropical wet-and-dry climates. The vegetation types include grassland, evergreen needle-leaf forest, deciduous broad-leaf forest, mixed forest, permanent wetland, open shrubland, closed shrubland, savanna, evergreen broad-leaf forest, and tundra. Stand age ranges from young seedlings to 500 years old (Paw U *et al* 2004). Sites from all ecosystem types with at least one year of complete NEE and meteorological data are included. NEE and meteorological data used in this analysis are taken from standardized files archived in the FLUXNET-LaThuile database which includes data from the AmeriFlux, Fluxnet-Canada, CARBOEUROPE, USCCC, ChinaFlux, OzFlux, CarboAfrica, and AsiaFlux networks. These data have been quality controlled and gap-filled by consistent methods (Papale *et al* 2006, Moffat *et al* 2007, Reichstein *et al* 2005). Meteorological variables used include air temperature, net radiation and precipitation. We have developed a new method to gap-fill the half-hourly meteorological data to produce reliable annual averages (see Methods in the supplementary data available at stacks.iop.org/ERL/5/034007/mmedia). In many cases, the site principal investigators have submitted revised annual NEE estimates based on more detailed, site-specific reanalyses. The data were used in this analysis only in those years when temperature, precipitation, net radiation, and NEE all met the gap-filling criteria (see Methods in the supplementary data available at stacks.iop.org/ERL/5/034007/mmedia).

Eddy-flux measurements are inherently uncertain due to: (1) advection errors caused by complex terrain (Aubinet *et al* 2005, Feigenwinter *et al* 2008) and complicated canopy structure (Yi 2008); (2) imbalance errors in the energy budget (Massman and Lee 2002, Foken 2008), and (3) the stochastic nature of turbulence (Hollinger and Richardson 2005, Moncrieff *et al* 1996). These errors have been studied intensively and remain to be quantified exactly for all sites (Reichstein *et al* 2007). The largest sources of uncertainty that have been quantified in a standardized way in annual NEE result from u^* filtering, gap-filling of missing data, and turbulent sampling errors (supplementary materials available at stacks.iop.org/ERL/5/034007/mmedia).

3. Grouping analysis

We hypothesize that two direct climatic controls on NEE, temperature and dryness (Budyko 1974), interact in complex ways with non-climatic or indirect climatic factors such as disturbance history, species, soil type and nutrient availability. Although it is not possible to develop a predictive global relationship of NEE with these variables, we ask does the dominant climate factor at individual sites follow distinct geographic patterns? While it is overly simplistic to argue that NEE is a function of two climate variables, it is possible to gain insight into global scale processes through the use of an objective statistical method to group sites by their dominant climate control.

We used a mixture regression model (see supplementary materials available at stacks.iop.org/ERL/5/034007/mmedia) to segregate sites into three groups (supplementary table S1 available at stacks.iop.org/ERL/5/034007/mmedia): (1) T-group: variations in NEE are best explained by mean annual temperature alone; (2) D-group: variations in NEE are best explained by a dryness index alone; and (3) B-group: NEE is co-limited by both mean annual temperature and dryness. An independent approach—a nonparametric kernel regression (Wand and Jones 1995) analysis of NEE against mean annual temperature and dryness for all three groups—provides a strong foundation for grouping the sites in this way. The pattern of contour lines in the contour plot for all 125 sites indicates a complex and mixed relationship for temperature and dryness (figure 1(a)), in which NEE at colder sites is generally a function of temperature and at warmer sites is generally a function of dryness. The kernel regression also confirms that the sites are successfully segregated according to their functional dependence. The contour plot for the T-group (figure 1(b)) shows that the contour lines are almost parallel to the dryness index axis. This implies that NEE is a monotonic function of temperature, and that the dryness index does not significantly influence the NEE of the sites in the T-group. The contour plot for the D-group (figure 1(c)) shows that the contour lines are almost parallel to the temperature axis. This implies that NEE is a monotonic function of the dryness index, and that the temperature does not significantly influence the NEE of the sites in the D-group. The contour plot for the B-group shows that the contour lines are neither parallel to the temperature axis nor parallel to the dryness index axis. This implies that both the temperature and the dryness index are contributors to the amount of NEE in the sites in the B-group. Moreover, NEE seems to linearly decrease as temperature increases or the dryness index decreases (figure 1(d)).

In the T-group, 84% of spatial variations in NEE can be explained by mean annual temperature (figure 2(a)), while in the D-group, 81% of spatial variation in NEE can be accounted for by a dryness index (figure 2(b)). However, in the smaller B-group, NEE is co-limited by mean annual temperature and dryness, and the correlations between the NEE and individual climate factors are relatively weak (figures 3(a) and (b)). We speculate that the variance in NEE unexplained by the climate factors in these three groups is primarily driven by non-climate factors such as stand age, disturbance history, species composition, or canopy leaf area index, reflecting local variation in nutrient and water availability (Raich *et al* 2002). These non-climate factors are also likely to play a role in the grouping algorithm and account for sites with similar temperature and dryness being grouped differently.

4. Discussion and concluding remarks

The empirical subdivision of groups also corresponds to latitudinal zonation (supplementary figure S1 available at stacks.iop.org/ERL/5/034007/mmedia): most sites of the temperature-limited group were located in the zones of

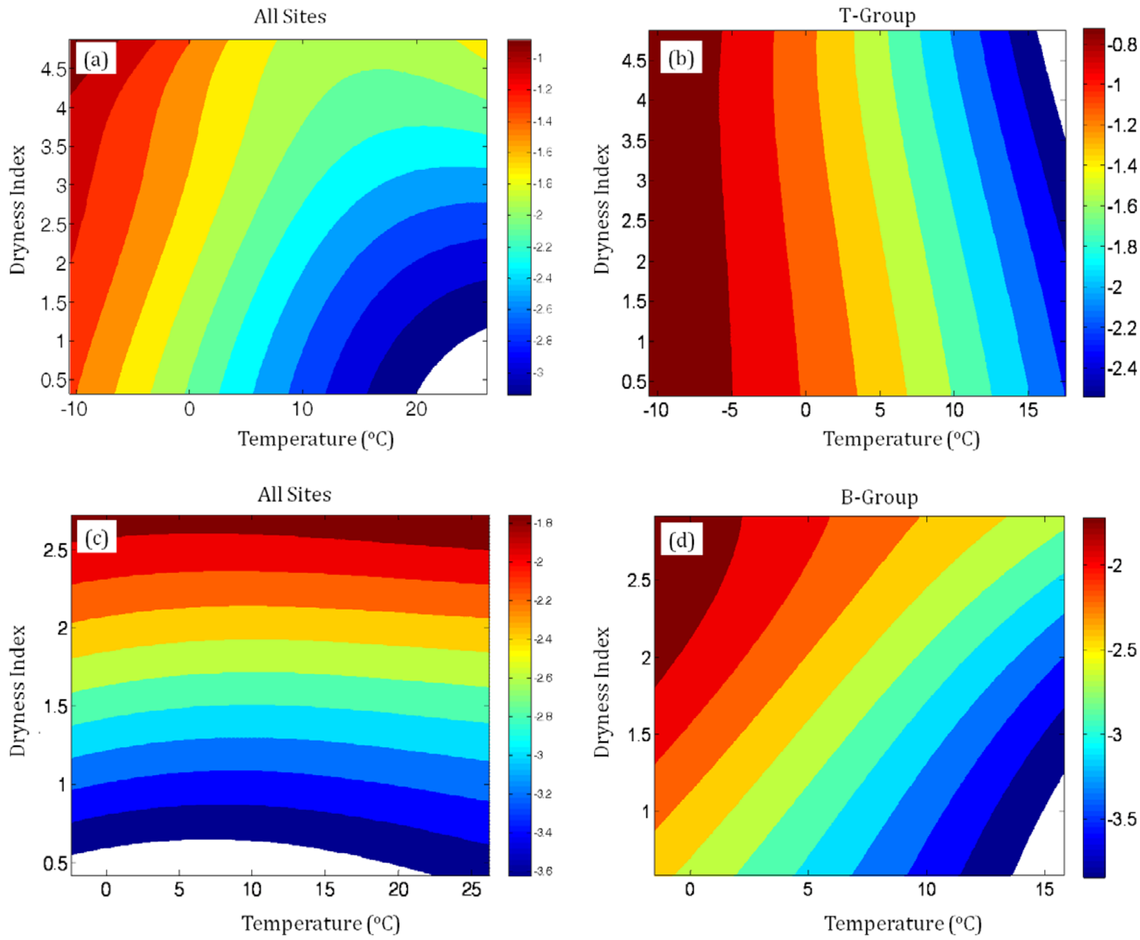

Figure 1. Contour plots of site-average NEE (tC ha^{-1} yr^{-1}) of: (a) all the 125 sites; (b) the T-group (47 sites); (c) the D-group (47 sites); and (d) the B-group (32 sites). These contour plots of the regression surface were produced by two-dimensional kernel regression (Wand and Jones 1995) based on the grouping data of the T-group, the D-group, the B-group, and the entire 125 sites (see Methods section and supplementary table S1 available at stacks.iop.org/ERL/5/034007/mmedia). The kernel regression is a commonly used nonparametric regression technique, which assumes the regression function is a smooth function of predictor variables rather than imposing a pre-specific functional form (parametric model) on the regression function.

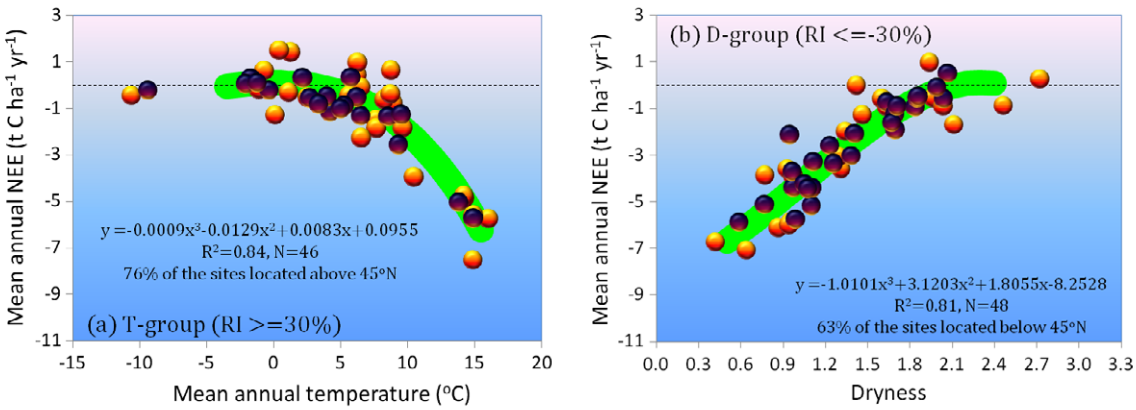

Figure 2. Climatic controls of the site-average net ecosystem exchange (NEE) across the FLUXNET sites (see supplementary table S1 available at stacks.iop.org/ERL/5/034007/mmedia): (a) temperature-limited group; and (b) dryness-limited group. The negative NEE values indicate that atmospheric carbon is assimilated by terrestrial ecosystems, while the positive NEE values indicate that terrestrial organic carbon is converted into atmospheric carbon. The filled circles with mango color in (a) are the site-average NEE of the sites in the prototype T-group with very high posterior probability (>99%) belonging to the temperature group, while the filled circles with mango color in (b) are the site-average NEE of the sites in the prototype D-group with very high posterior probability (>99%) belonging to the dryness group (see the Methods section and supplementary table S1 available at stacks.iop.org/ERL/5/034007/mmedia). The thick green lines represent model predictions.

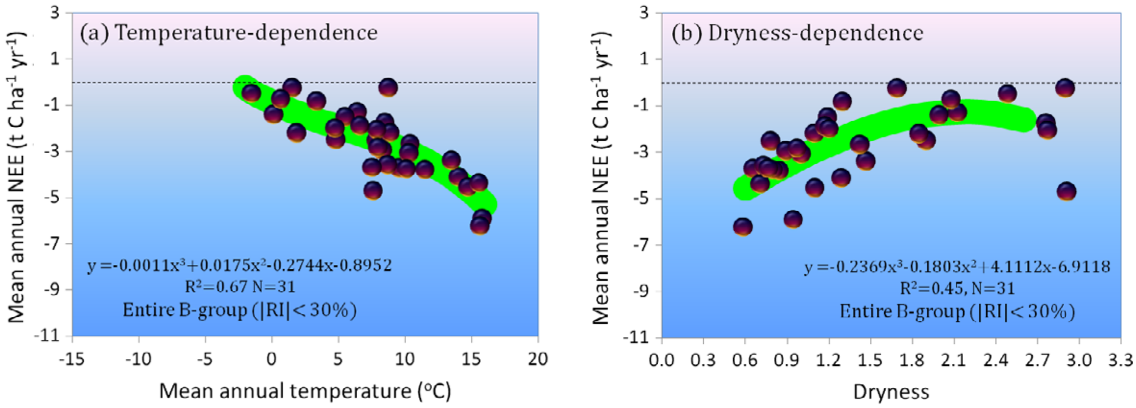

Figure 3. The site-averaged NEE of B-group sites that are sensitive to both: (a) temperature and (b) dryness.

temperate and boreal climate (76% are located above 45°N, supplementary figure S2(a) available at stacks.iop.org/ERL/5/034007/mmedia), while most sites of the dryness-limited group were located in the zones of subtropical climate (63% are located below 45°N, supplementary figure S2(b) available at stacks.iop.org/ERL/5/034007/mmedia). The B-group sites were almost symmetrically distributed around 45°N (supplementary figure S2(c) available at stacks.iop.org/ERL/5/034007/mmedia). The controlling function of temperature for terrestrial carbon exchanges breaks down as mean annual temperature approaches 16 °C. All sites with mean annual temperature above 16 °C are in the dryness group (figures 2(a) and 3(a)). Our findings suggest that NEE at mid-to-high latitudes is controlled largely by the mean annual temperature, while at mid-to-low latitudes, it is controlled largely by dryness. The geographic region around 45°N is a transition zone where many sites are co-limited by both temperature and dryness.

The global empirical patterns of NEE driven by climate gradients found in this paper are partially supported by another global data analysis conducted by Nemani *et al* (2003) based on correlation between 18 years climate data and net primary production (NPP) derived from spatially continuous satellite data. This modeling study found that NPP is largely controlled by temperature at mid-to-high latitudes, while at subtropical and tropical it is controlled by radiation and water, i.e. by dryness (ratio of net radiation to precipitation) as was used in our analysis. Even though the predicted ecological variables used here (NEE) and in Nemani *et al* (2003)'s analysis (NPP = NEE − soil respiration) were not the same, the consistent climate-driven spatial patterns derived from the two independently global datasets at least indicates that climate control plays an important role in the terrestrial carbon cycle. On the other hand, it is noted that our findings are different from the individual site analyses on climate control of NEE (e.g. Dunn *et al* 2007). These analyses study the temporal variability of NEE based on the measurements from a single site, i.e. how climate factors drive NEE changes from year to year. Our analysis studies the spatial variability of NEE based on measurements from many sites, i.e. how spatial gradients of climate drive NEE changes from location to location. Our data analysis demonstrated that spatial variability of NEE is 2.5 times greater than temporal variability of NEE (see discussion in section 3 of supplementary materials available at stacks.iop.org/ERL/5/034007/mmedia). Therefore, the existing differences between temporal variability and spatial variability are expected.

Why is the average annual temperature the main climate driver of NEE at mid- and high-latitudes? The most likely reason is that higher average annual temperature also reflects prolonged growing seasons in cold climate regions and hence increases carbon uptake in biomass (White *et al* 1999, Malhi 2002, Kato and Tang 2008) relative to heterotrophic decomposition. At many sites, respiration rates lag NPP rates proportionally after disturbance, and a larger NPP resulting from a longer growing season contributes to higher uptake (Goulden *et al* 1996, Leuning *et al* 2005). In the absence of other factors, we therefore expect higher carbon uptake at warmer sites within the temperature group. This speculation is partially supported by previous studies with limited data (Goulden *et al* 1996, Leuning *et al* 2005). In warm climate regions (low-latitudes), growing season length is less likely to be affected by temperature variations because these regions either experience a year-round growing season or a growing season that is limited by factors other than temperature, mainly water stress. The global-biome-climate data analysis (Zhou *et al* 2008) indicates that the mean annual temperature of C4 grassland biome is about 23 °C, in other words it is much larger than the threshold value of 16 °C, and hence C4 sites are much more likely to be in a dryness group according to our findings above. It is well known in physiology that the assimilation of C4 ecosystems, which resides mainly in the subtropical regions (Ehleringer *et al* 2005), is independent of temperature but is limited by water stress (Lambers *et al* 1998). This fact partially supports our findings that the NEE-driver of a site with mean annual temperature larger than 16 °C is likely to be dryness and such sites are likely located in tropical or subtropical regions.

The majority of the 125 sites are recovering from past disturbance rather than being actively disturbed, and thus are in the 'slow in' instead of the 'rapid out' phase of carbon flow in the terrestrial biosphere as conceptualized by Korner (2003). Disturbance history and stand age play a large role in NEE variability (Amiro *et al* 2010), which is seen at chronosequence sites with similar climates (Ryan and Law 2005). Though the temperature and dryness groups are correlated well with their respective indices, the overlap of the two groups in temperature–dryness space suggests that NEE is controlled by a complex interaction of climate and non-climate factors. Our results do not support the recent suggestion that a single abiotic factor such as nitrogen supply dominates NEE (Magnani *et al* 2007, Sutton *et al* 2008).

Links between terrestrial CO_2 exchanges and climate controls are clearly demonstrated by many site-years of data from the eddy-flux tower networks. Our findings are essential to understand how future climate change may affect terrestrial CO_2 exchanges with the atmosphere in the 21st century (Qian *et al* 2010). In the IPCC 2007 report, projected warming in the 21st century is expected to be greatest over land and at high northern latitudes, while projected decreases in precipitation are likely in most subtropical land regions (IPCC 2007). Although climate controls on long-term changes in NEE may be different from controls on spatial variability of NEE, our results imply that the most likely future climate change scenarios could strongly intensify terrestrial CO_2 uptake in high-latitudes and weaken CO_2 uptake in low-latitudes.

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