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A temperature threshold to identify the driving climate forces of the respiratory process in terrestrial ecosystems

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ABSTRACT

Terrestrial ecosystem respiration (R_e) is the second largest carbon flux between the biosphere and atmosphere. Therefore, climate-driven changes of R_e greatly impact on future atmospheric CO_2 concentration. The aim of this study was to derive an air temperature threshold to identify the driving climate forces of the respiratory process in terrestrial ecosystems within different temperature zones. A global dataset of 647 site-years of ecosystem flux data and related variables were collected at 152 sites. The quantile regression was applied to evaluate relationships between the maximum realizable R_e rates and mean annual air temperature (MAT) as well as other micrometeorological factors (i.e., atmospheric CO_2 concentration, atmospheric water content, soil heat flux, sensible heat flux, latent heat flux, precipitation, relative humidity, and soil water content). Our analysis revealed an ecosystem threshold of MAT of 11 ± 2.3 °C. In ecosystems with MATs lower than the threshold, the maximum R_e rates were primarily dependent on temperature and respiration was mainly a temperature-driven process. In ecosystems with MATs higher than the threshold, besides MAT, other factors, such as water availability and surface heat flux, became significant driving forces of the maximum R_e rates and respiration was a multi-factor-driven process. Temperature played the key role in generation of the maximum R_e rates in the terrestrial ecosystems, while other driving forces reduce the maximum R_e rates and the temperature sensitivity of the respiratory process. According to a regression tree analysis, MAT was also the most influencing factor of mean R_e rates among the climate forces. The information from this study should be useful to predict the respiratory process in terrestrial ecosystems with different temperatures under the climate change.

1. Introduction

Among the greenhouse gases, carbon dioxide (CO_2) contributes the most to the contemporary climate change [1]. Terrestrial ecosystem respiration (R_e) is a major source of CO_2 release and the second largest carbon flux between the biosphere and the atmosphere [2]. Therefore, climate-induced change in R_e should profoundly impact the global carbon cycle.

Biotic and abiotic factors can be various driving forces of ecosystem respiration [3]. Temperature is considered as the most prominent factor to determine the natural distributions of plants and to regulate activities of microbial communities among climatologic factors [4]. It has been shown that R_e rates increase exponentially with temperature [5], while this temperature relationship can be modified by many variables at the ecosystem level [6]. According to the metabolic theory of ecology, the temperature dependence of R_e can be quantified by a constant activation energy ($E = 0.60$ eV) [5,7]. By contrast, other studies revealed varied average E values of R_e with ecosystem types and

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climate zones [8].

Temperature sensitivity of R_e rates is commonly quantified using the Q_{10} index (the proportional increase in respiration per 10 °C rise). Mahecha et al. (2010) [6] showed that Q_{10} values of R_e were independent of temperature and converged on a constant value (1.4 ± 0.1) across biomes. Constant Q_{10} values of R_e have been utilized in several ecosystem models [9]. On the contrary, it has been reported that Q_{10} values vary in different temperature ranges at the microbial community level [10]. Also, Q_{10} values have been shown to change with different ecosystem types or different vegetation types within an ecosystem [8].

The apparent inconsistencies in the literature about the ecosystem respiration process are mostly attributed to the combined effects of different driving forces on the process. As a result, temperature may be the dominating driving force of the respiration process in some ecosystems, while other environmental factors can also significantly impact the process in other ecosystems [11]. It has been reported that some micrometeorological factors can affect the assimilatory process of plants and therefore the substrate quantitity and quality for respiration [12]. In particular, water availability (e.g., soil water content and precipitation) can become one of controlling factors of R_e in certain temperature regimes [13]. However, it is still unclear how different climatic factors affect the respiratory process in terrestrial ecosystems.

The concept of ecological threshold has been widely recognized as an important paradigm to assess the effect of environmental limiting factors on biological processes [14]. As a turning point, the ecological threshold divides the ecosystems into two groups, between which the driving forces of ecological process are different [14]. The ecological threshold is also linked to alternatively stable states in the structure and function of ecosystems. Therefore, the alternatively stable states represent different combinations of ecosystem components (e.g., assemblage of species, productivity) and environmental conditions that may stably persist at certain spatial and temporal scales [15]. According to the concept, if R_e rates are only dependent on temperature (i.e., the temperature-driven pattern), the maximum realizable R_e rate (i.e., the upper bound of R_e rate) should increase with MAT. If other micrometeorological factors as well as temperature control R_e rates, the change of maximum realizable R_e rate with MAT (i.e., the multi-factor-driven pattern) is expected to be different from the temperature-driven pattern.

Given the review of R_e and the concept of ecological threshold, we hypothesized that there should be a temperature threshold that can be utilized to identify the driving climate forces of the respiratory process in terrestrial ecosystems within different temperature zones. Therefore, the objectives of this study were to investigate the effects of air temperature and other micrometeorological factors, including greenhouse gases (e.g., atmospheric CO_2 concentration and atmospheric H_2O content), heat flux (e.g., soil heat flux, sensible heat flux, and latent heat flux), and water availability (e.g., precipitation, relative humidity, and soil water content), on R_e at different latitude regions and to quantify the temperature threshold for respiratory process in different terrestrial ecosystems.

2. Materials and methods

2.1. Data

This study was carried out using the following data sources: FLUXNET Database (http://www.fluxdata.org/, Open Data set), European Flux Database (European Fluxes Database Cluster http://gaia.agraria.unitus.it/), AmeriFlux (http://ameriflux.lbl.gov/), Distributed Active Archive Center for Biogeochemical Dynamics (ORNL DAAC http://daac.ornl.gov/), AsiaFlux (http://asiaflux.net/), and JapanFlux (FFPRI Fluxnet http://www2.ffpri.affrc.go.jp/labs/flux/). In case of overlap between different databases, the larger (or largest) database was chosen as the primary source. In total, 647 site-years data were collected at 152 eddy flux sites globally. The database covering broad environmental gradients and basic information of the database, including site ID, latitude, longitude, PFT, climate class, year of data collection, and reference of each data set, are listed in Table A.1 (Supplementary Material). Annual ecosystem respiration rates were estimated from the mean NEE values measured during nighttime. At least five data points for each day and at least 255 measurements in each site were required for the estimation [6]. Mean annual air temperatures (MAT) and other mean annual values of selected micrometeorological factors (i.e., greenhouse gases, heat flux, and water availability), including atmospheric CO_2 concentration (denoted by CO_2), atmospheric H_2O content (H_2O), soil heat flux (G), sensible heat flux (H), latent heat flux (LE), precipitation (P), relative humidity (RH), and soil water content (SWC), over the same periods for CO_2 flux measurements were used as the corresponding data for analysis.

2.2. Data analysis

Based on the aforementioned hypothesis, the quantile regression was applied to evaluate relationships between the maximum realizable R_e rates and MAT as well as other micrometeorological factors (i.e., CO_2, H_2O, G, H, LE, P, RH, and SWC). Because of complex interactions among the factors affecting ecological processes, the concept of ecological limiting factors often focuses on the quantile slope near the maximum response [16]. Following the procedure of Cade and Noon (2003) [16], we applied the quantile linear regression at the quantile levels of $\tau \in (0.90, 0.95, 0.99)$ to evaluate relationships of the maximum realizable R_e rates vs. temperature and other micrometeorological factors. For a tested factor, if quantile slopes at all τ levels are significantly different from zero, the maximum realizable R_e rates are significantly correlated to the factor. If the correlation (i.e., positive or negative) trends between the maximum realizable R_e rates and a factor at the three linear quantiles are not consistent, the quantile linear regression should be further tested at more quantiles. Many changes in ecological processes occur with gradual transitions [17]. Thus, a bent-cable model was used to describe the gradual changes from one ecological state to another to form a piecewise linear model [18]. According to the concept of ecological threshold [14], the quantile regression analysis was used to determine the temperature threshold of R_e rates. The model was implemented in the 'quantreg' library in the statistical package R (http://www.r-project.org).

In addition to analyzing patterns of the maximum R_e rates, a regression tree analysis was conducted to determine the effects of temperature and other micrometeorological factors on the mean realizable R_e rates. By repeatedly dividing the data into more homogeneous groups, the regression tree method can be used to exam the relative importance of temperature and other micrometeorological factors in regulating R_e rates [19]. After tree construction, cross-validation procedures were used to refine the trees to better represent relationships among the variables [19]. The regression tree analysis was implemented in 'rpart' library in the statistical package R.

3. Results

3.1. Relationship between the maximum realizable R_e rates and MAT

Using the quantile piecewise linear regression at $\tau = 0.99$, we evaluated the upper bound of R_e rates (i.e., the maximum realizable R_e rates) changing with MAT. As shown in Fig. 1, a threshold of MAT was identified as 11 ± 2.3 °C. In ecosystems with a MAT range below the threshold, the relationship between the maximum realizable R_e rate and MAT was characterized with a linear equation $R_e = 0.19\,(MAT) + 2.49$. In ecosystems with MAT > 11 ± 2.3 °C, the relationship between the maximum realizable R_e rates and MAT was characterized with a linear equation $R_e = 0.07\,(MAT) + 3.81$.

According to the MAT threshold, terrestrial ecosystems across the