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Seasonally different response of photosynthetic activity to daytime and night-time warming in the Northern Hemisphere

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Abstract

Over the last century the Northern Hemisphere has experienced rapid climate warming, but this warming has not been evenly distributed seasonally, as well as diurnally. The implications of such seasonal and diurnal heterogeneous warming on regional and global vegetation photosynthetic activity, however, are still poorly understood. Here, we investigated for different seasons how photosynthetic activity of vegetation correlates with changes in seasonal daytime and night-time temperature across the Northern Hemisphere (>30°N), using Normalized Difference Vegetation Index (NDVI) data from 1982 to 2011 obtained from the Advanced Very High Resolution Radiometer (AVHRR). Our analysis revealed some striking seasonal differences in the response of NDVI to changes in day-versus night-time temperatures. For instance, while higher daytime temperature (T_{max}) is generally associated with higher NDVI values across the boreal zone, the area exhibiting a statistically significant positive correlation between T_{max} and NDVI is much larger in spring (41% of area in boreal zone – total area 12.6×10^{6} km^{2}) than in summer and autumn (14% and 9%, respectively). In contrast to the predominantly positive response of boreal ecosystems to changes in T_{max}, increases in T_{max} tended to negatively influence vegetation growth in temperate dry regions, particularly during summer. Changes in night-time temperature (T_{min}) correlated negatively with autumnal NDVI in most of the Northern Hemisphere, but had a positive effect on spring and summer NDVI in most temperate regions (e.g., Central North America and Central Asia). Such divergent covariance between the photosynthetic activity of Northern Hemispheric vegetation and day- and night-time temperature changes among different seasons and climate zones suggests a changing dominance of ecophysiological processes across time and space. Understanding the seasonally different responses of vegetation photosynthetic activity to diurnal temperature changes, which have not been captured by current land surface models, is important for improving the performance of next generation regional and global coupled vegetation-climate models.

Introduction

Vegetation is an important component of the Earth system, playing an important role in modulating regional and global climate change through biogeochemical and biophysical feedbacks (Field et al., 2007; Peñuelas et al., 2009). Biological characteristics of vegetation, such as photosynthetic capacity, length of the growing season, and plat population dynamics are usually sensitive to climate change (Myneni et al., 1997; Root et al., 2003 ; Adams et al., 2009; Peñuelas et al., 2013). Over the last decades, annual trends in NDVI and in the amplitude of the annual fluctuations in atmospheric CO2 concentration (Graven et al., 2013) both indicate that global change has promoted photosynthetic activity and growth of vegetation across the Northern Hemisphere (Keeling et al., 1996; Peng et al., 2011). In temperate and boreal regions, photosynthetic activity is typically characterized by a marked seasonal cycle. Because the consecutive phenological and ontogenetic stages are dominated by different ecophysiological processes, also the climatic requirements may vary across the different phenological stages. Hence, the response of vegetation photosynthetic activity to climate variations is dependent upon season (Xu et al., 2003; Yu et al., 2003; Richardson et al., 2010). In its latest Assessment Report, the Intergovernmental Panel of Climate Change (IPCC) Assessment Report provides further evidence that climate warming is asymmetric among different seasons and continents (IPCC, 2013). For instance, the seasonality of temperature is diminishing at high latitudes because of faster warming in winter and spring than in summer (Xu et al., 2013). Similarly, night-time temperatures have been increasing faster than daytime temperatures globally since 1950s, although this phenomenon is not temporally or spatially uniform in observation (IPCC, 2013). A better understanding about the implications of such diurnal and seasonal asymmetry in global warming on regional and global vegetation photosynthetic activity will be helpful for improving our quantification of global vegetation response to climate change in the past and the future (Still, 2013).

Here we present an analysis, separately for spring, summer and autumn, of how vegetation photosynthetic activity is associated with changes in daytime and night-time temperature across the northern Hemisphere (>30°N) from 1982 to 2011, using time series data set of the Normalized Difference Vegetation Index (NDVI) obtained from the Advanced Very High Resolution Radiometer (AVHRR) and associated climate datasets. Although some other recent modern satellite products, such as FPAR and LAI (Myneni et al., 2002, Baret et al., 2007), may be better in measuring photosynthetic activity, these products have not been available for a sufficiently long period. The data set of the AVHRR-NDVI, by contrast, has been widely considered a useful synthetical integrator of the environmental conditions that regulate phenology and productivity (Pettorelli et al., 2005; Piao et al., 2006; Zeng et al., 2013) for three decades. Analyses of field experiments (Penuelas et al., 2004; Wan et al., 2009) and satellite observations (Peng et al., 2013; Xia et al., 2014) have shown that day- and night-time warming could have different impacts on growing-season mean NDVI because the direct and indirect mechanisms by which temperature impacts on productivity differ between day and night. Given that different ecophysiological processes dominate plant activity in different phenological stages, one can also expect the response of NDVI to day- and night-time warming to vary among seasons. Thus, seasonal variation in vegetation response to global warming may add to the complexity of the phenomenon discovered by Peng et al. (2013), while on the other hand it may also provide clues to better understand the geographical differences in the productivity response to daytime and night-time warming. Such information, however, has not been extensively documented in the literature. It is therefore our primary goal to understand how changes in daytime and night-time temperature during different seasons influence the vegetation photosynthetic activity of the northern temperate and boreal regions. Documenting the seasonal variation in the impacts of daytime and night-time warming on vegetation photosynthetic activity provides us a better understanding of how current and future climate change may impact on vegetation activity and thereby on the global carbon cycle, and is critical for efficient vegetation management in a rapidly changing world. A second objective of this study is to assess whether or not these satellite-based ecosystem responses to the uneven warming are captured by two global land surface models: ORCHIDEE (Krinner et al., 2005) and NCAR_CLM4CN (Oleson et al., 2010).

Materials and methods

Datasets

We used the third generation NDVI dataset produced by the Global Inventory Monitoring and Modeling Studies (GIMMS) group for the period of January 1982 to December 2011 (Pinzon et al., 2013). These data are generated at 1/12 degree and composited over approximately 15 days periods with the Maximum Value Compositing Technique (Holben et al., 1986). This data set has been calibrated for sensor changeover (satellite sensor systems have experienced many changeovers: from NOAA 7 to NOAA 9, from NOAA 9 to NOAA 11, from NOAA 11 to NOAA 14, from NOAA 14 to 16, and from NOAA 16 to 18), and corrected against sensor degradation, satellite orbit drift and changed solar zenith angles (Zhou et al., 2001; Tucker et al., 2005; Luo et al., 2013). Compared with previous versions of the GIMMS NDVI datasets, this version has improved in data quality, particularly in high latitudes where the growing season is shorter. To further eliminate noise and bias caused by clouds, atmospheric disturbance and changes in solar angle (Holben 1986; Tucker et al., 2005), we used monthly NDVI values, which were determined as the maximum value of the two NDVI composites of each month. This data set has recently been successfully applied for detecting changes in vegetation photosynthetic activity (Peng et al., 2011; Xu et al., 2013).

The climate data (maximum daily temperature (T_{max}), minimum daily temperature (T_{min}), precipitation, shortwave solar radiation) used in this study covered the period 1982-2011 and had a spatial resolution of 0.5 degree. These data were monthly aggregated from the CRU TS 3.20 climate dataset obtained from the Climate Research Unit (CRU), University of East Anglia (Mitchell & Jones, 2005) and the 0.5 degree CRU-NCEP data set (1901-2010), which is a combination of CRU TS.3.2 0.5 degree monthly climatology data and 2.5 degree National Centre for Environmental Prediction (NCEP2) reanalysis data from 1948 to near real time. Due to the lack of observed solar radiation data during the study period, we used cloud data (CRU) as surrogates of observed solar radiation.

Carbon Cycle models

Two process-based land surface models simulated leaf area index (LAI) and carbon fluxes (gross primary productivity, GPP; net primary productivity, NPP) with a spatial resolution of 0.5 degree for the period from 1982 to 2010. These two models are ORCHIDEE (Krinner et al., 2005) and NCAR_CLM4CN (Oleson et al., 2010; Lawrence et al., 2011), which both have been widely used to investigate regional and global land carbon fluxes (e.g. Sitch et al., 2008), as well as their responses to climate change and their feedbacks to the climate system (Thornton, et al., 2007). Models were forced with reconstructed historical climate fields and rising atmospheric CO_2 concentration. Both models used the same climate forcing files from the CRU-NCEP v4 dataset with 6 hourly time step (http://dods.extra.cea.fr/data/p529viov/cruncep/).

Analyses

Partial correlation analysis was used to statistically distinguish the influence of interannual changes in T_{max} and T_{min} on vegetation NDVI across different seasons. Partial correlation yields the correlation between two variables, while controlling for a third or more variables (Kendall 1946, Baba et al., 2004). If the partial correlation approaches 0, the inference is that any direct correlation was spurious. Since precipitation and solar radiation may also influence NDVI (Nemani et al., 2003), variations in precipitation and cloudiness were also taken into account in the partial correlation analysis. NDVI and all relevant climate variables were detrended by a linear detrending method (Peng et al., 2013) before the partial correlation analysis. We also used the LAI, GPP and NPP output of the two land surface models to verify whether these models can capture the same relationships between vegetation photosynthetic activity and T_{max} and T_{min}, as indicated by the remote sensing-based analyses. Note these two models are forced with climate data from the CRU-NCEP, instead of that from the CRU. Accordingly, T_{max} and T_{min} from the CRU-NCEP are used for the partial correlation analysis of the model simulated results.

Following Zhou et al. (2001), we defined the spring, summer, and autumn seasons as the periods from April to May, June to August, and September to October, respectively. To ensure the robustness of the estimated temperature sensitivity of seasonal NDVI to these season definitions, we repeated the analyses with modified definitions of spring, summer, and autumn; as the period from May and June, July to August, and September and October, respectively; and as the period from green-up to maturity, maturity to senescence and senescence to dormancy respectively. The transition dates for those key phenological phases have been derived by MODIS dataset (Zhang et al., 2003) and the months where multi-year averaged transition dates located are the boundaries for each season period.

Results

During spring, vegetation NDVI in the Northern Hemisphere was predominantly positively correlated with daytime temperature (T_{max}) change (Fig.1a). However, these responses clearly differed between latitudinal zones. In the boreal zone (>50°N), 89% of the land area showed a positive correlation between NDVI and T_{max} (red lines in Fig.2a). Although this correlation was statistically significant only in about 41% of the area, significant negative correlations between NDVI and T_{max} did not occur during spring (red lines in Fig.2a). In contrast to the boreal zone, during spring the temperate regions (30°N-50°N) showed a statistically significant positive correlation between NDVI and T_{max} only in 12% of the land area (red lines in Fig.2b). These significant positive spring-time correlations between NDVI and T_{max} in the temperate zone were found mainly in the wetter or cooler regions, such as western America, southern China and the Tibetan Plateau (Fig.1a, Fig. S1). In addition, negative correlations between NDVI and T_{max} did occur during spring in some temperate areas, mostly in arid and semi-arid regions, such as Central North America, temperate China and Central Asia (Fig.1a, Fig. S1), although only a small fraction of these were statistically significant.

While in springtime the correlation of NDVI with T_{min} was predominantly negative, especially in the boreal zone, night-time warming exhibited a strikingly different pattern (Fig.1b). First, vegetation NDVI correlated more frequently negatively than positively with T_{min} in the boreal regions (Fig. 1b and red lines in Fig. 2c). Many boreal areas in which NDVI correlated positively with T_{max}, correlated negatively with T_{min}. A similar observation can be drawn for the temperate zone: areas that tended to correlate positively with T_{max}, correlated negatively with T_{min} (mainly wet or cool temperate regions), and vice versa in the arid and semi-arid regions (compare Fig. 1a with Fig.1b; Fig. S1).

During summer, NDVI was less responsive to interannual changes in T_{max} or T_{min} (Fig. 1c, 1d) than in spring. In boreal regions, summer NDVI remained positively correlated with T_{max} in most areas, but the correlation was statistically significant only in 14% of the area (Fig.1c, 2a). In temperate regions, however, summertime daytime warming was negatively correlated with vegetation NDVI in a much larger area than in spring (compare Fig.1c with Fig. 1a). The negative correlation between summer NDVI and T_{max} was found to be statistically significant in 9% of the temperate zone, primarily in arid, semi-arid and cool regions, such as Central Asia, temperate China, Central America and Tibetan Plateau (Fig.1c, 2b and S1).

Changes in T_{min}, on the other hand, showed a roughly similar impact on NDVI during summer as compared to spring, although differences did occur (compare Fig.1d with Fig. 1b). Overall, both in the boreal and in the temperate zone, half of the area exhibited a positive correlation between NDVI and T_{min}, and the other half showed a negative correlation between them (compare green lines in Fig. 2c and 2d). For example, negative correlations between summer NDVI and T_{min} were found in eastern Europe, southern Siberia, Mediterranean, western America, as well as wet temperate regions, while positive correlations between them were mainly found in arid, semi-arid and cool temperate regions (Fig.1d, S1).

During autumn, the spatial pattern of the NDVI correlations to changes in T_{max} roughly resembled the springtime pattern in the temperate zone, while in the boreal zone it closely resembled the summertime pattern (compare Fig. 1e with Figs. 1a and 1c). Across the entire Northern Hemisphere, statistically significant positive correlations were found in only 9% of the area (Fig.2a and 2b). It should also be noted that, in autumn, significant negative correlations between T_{max} and NDVI were very uncommon, occurring only in Central North America and Eastern Europe.

In contrast to the observed correlations between NDVI and T_{max}, the autumnal pattern of the correlation between NDVI and T_{min} did exhibit more widespread negative correlations and much fewer positive correlations as compared to spring or summer (Fig. 1f, Fig. 2c and 2d). Negative correlations outshadowed the positive correlations in both the temperate and boreal zones, but were especially common in Siberia (Fig.1f).

Note the high inter-correlation between T_{max} and T_{min} makes the partial correlation results difficult to interpret, we also conducted an supplementary partial correlation analysis in which detrended T_{max} and T_{min} were replaced with their average (T_{mean}=(T_{min}+T_{max})/2) and difference (DTR= T_{max}-T_{min}) (Fig. S2). A significant partial correlation between NDVI and DTR is found for all the three seasons. For example, in boreal regions, NDVI is predominantly positively correlated with DTR in spring; while in dry temperate regions, the partial correlation between NDVI and DTR is negative in summer but positive in autumn. This significant partial correlation between NDVI and DTR again confirms the finding that vegetation growth responds differently to changes in T_{max} and T_{min}.

We next examined, in the different seasons, the correlations between model-simulated LAI and GPP and interannual changes in the corresponding temperature variables. The specific spatial and seasonal patterns of these correlations are shown in Fig. 3. Simulations with ORCHIDEE suggested that rising T_{max} is generally associated with higher simulated GPP in the boreal zone and the Tibetan Plateau, a correlation that is particularly strong in spring and autumn, and weaker in summer. CLM4 showed a much smaller area with a positive response of GPP to daytime warming than ORCHIDEE. However, neither ORCHIDEE, nor CLM4 simulated the seasonal dynamics of the impact of T_{min} changes on GPP (significant at 95% confidence level based on paired-samples t-tests) that the NDVI data exhibited. Among all the three seasons, positive correlations between GPP and T_{min} were found in some boreal regions, mainly where GPP was also positively correlated with T_{max}. Model simulated NPP showed similar spatial patterns in the responses to changes in T_{max} or T_{min} as that of GPP (Fig. S3). Model simulated LAI also responded differently to changes in T_{max} or T_{min} as compared with the NDVI-response and the models were not in good agreement (Fig. 4).

Discussion

This study explored the seasonal variation in the response of vegetation photosynthetic activity to daytime and night-time temperature changes in the temperate and boreal regions of the Northern Hemisphere, an area with a globally important land carbon sink (Myneni et al,. 2001; Pan et al., 2011). In line with results from an earlier study based on annual variables (Peng et al., 2013), we observed that over the last three decades higher inter-annual T_{max} have been generally associated with higher vegetation activity, especially in the high latitude regions. The current study now shows that the strength of the relationship between T_{max} and NDVI varies among seasons. Among the three seasons, spring shows the largest area with a significantly positive relationship between T_{max} and NDVI (Fig. 1). In addition to increased soil nitrogen mineralization and availability (Shaw and Harte, 2001; Melillo et al., 2011; Hietz et al., 2011), a temperature-driven phenological shift towards earlier and longer growing seasons has been suggested to be one of the most important mechanisms for promoting northern vegetation photosynthetic activity (greening) under global warming (Myneni et al., 1997; Tucker et al., 2001; Piao et al., 2007). The weaker correlation between T_{max} and NDVI during autumn compared with spring could be linked to either lower soil moisture, surface soil frost in some regions, less radiation or plant senescence in the autumn season (Robock et al., 2000; Nijssen et al., 2001; Gauslaa et al., 2005; Zhang et al.,2013). It has been suggested that the temperature sensitivities of duration of the photosynthetic season in autumn and of autumn productivity are both smaller than that of their spring counterparts (Piao et al., 2008; Richardson et al., 2010; Chapman, 2013). In addition, one day lengthening of the growing season increases productivity more during spring more than during autumn, as expected from the longer days and higher radiation during spring (see e.g., Richardson et al., 2010). To investigate potential biases caused by different definitions of seasons in this analysis, we tested two other definitions of the three seasons (see Methods) and the results confirm the observed spatial patterns of the NDVI responses to T_{max} or T_{min}, although there is slight variability in the significant percentage about the response of vegetation to T_{max} or T_{min} (Figs. S4 and S5).

We observed that positive anomalies in T_{max} were associated with smaller gains of vegetation productivity in summer than in spring or autumn. Although it is known that the optimum temperature for photosynthesis is higher in summer than in spring or autumn (Berry and Björkman, 1980), our analysis therefore suggests that, summer maximum temperature in most areas is close to the optimal value for plant photosynthetic activity (Wan et al., 2005). An alternative explanation for the smaller NDVI response to T_{max} in summer than that in spring or autumn is associated with the saturation of NDVI over dense vegetation, which is more likely to occur in summer (Fensholt et al., 2012). To test this hypothesis, we plotted the percentages of areas with insignificant partial correlation ($P>0.05$) between NDVI and Tmax during summer along the gradient of NDVI values (Fig. S6). The result, however, does not support the idea that sparse vegetation is less saturated and therefore more sensitive to the change in Tmax than dense vegetation (Fig. S6a). The same result is also observed when pixels with only positive or negative NDVI responses to T_{max} are singled out (Fig. S6b, c). Therefore, the observed reduction in summertime NDVI sensitivity to Tmax is unlikely to be caused by the NDVI saturation effect of more closed vegetation.

Our results further suggest that in contrast to most high-latitude ecosystems, increases in T_{max} negatively influence vegetation photosynthetic activity in temperate dry regions, particularly during summer. This negative temperature sensitivity in temperate dry ecosystems may result from increased water stress via warming-induced soil moisture reduction (Llorens et al. 2004; Williams et al., 2012; Xu et al., 2013). This hypothesis is supported by the positive correlation ($P<0.05$) between the response of NDVI to T_{max} and the multi-year averaged topsoil water content over 1988-2007 in all the three seasons (Owe et al., 2008, Fig. S7). In addition, vapor pressure deficit (VPD) exponentially increases with rising T_{max}, which can further reduce soil moisture through increasing transpiration (Williams et al., 2012). The enhanced VPD coupled with reduced soil moisture can lower the duration of stomatal openness and increase the risk of hydraulic failure, and consequently reduce vegetation growth rate (Williams et al., 2012). On the other hand, reduced vegetation growth, in turn, can create an additional warming effect through the reduction in transpiration demand which increases radiation partitioning into sensible heat flux (Jeong et al., 2009). This positive feedback may further amplify the negative NDVI sensitivity to changes in T_{max} in a warming season. Thus the complex interaction between T_{max}, soil moisture, plant transpiration and growth rate makes soil moisture an important driving factor in regulating vegetation photosynthetic activity over the dry temperate regions in summer (Ciais et al., 2005; Williams et al., 2012; Vicente-Serrano et al., 2013). Furthermore, there is increasing evidence from both field experiments and modeling studies that rising temperature can significantly change soil water availability in the root zone (Llorens et al., 2004; Huntington 2006; Xu et al., 2013), and thereby negatively affect vegetation photosynthetic activity (Peñuelas et al., 2004; Angert et al., 2005).

In both spring and autumn, the impact of reduced soil moisture on vegetation photosynthetic activity may be partly canceled out by positive warming-induced effects, such as extended growing seasons, or may be irrelevant because plant available water remains well above wilting point. This may explain the lack of negative correlation between T_{max} and NDVI in spring and autumn across the temperate zone.

Compared to daytime warming, nighttime warming has been found to have a smaller negative influence on soil moisture (Xia et al., 2009; Peng et al., 2013). Therefore, the indirect effect of nighttime warming via a change in soil moisture is probably smaller than that of daytime warming. Similar to daytime warming, night-time warming may also impact on vegetation photosynthetic activity in opposite ways, through the action of different mechanisms. First, night-time warming can stimulate plant photosynthesis (Beier et al., 2008; Wan et al., 2009) through increased draw-down of leaf carbohydrates at night (Turnbull et al. 2002, 2004). Second, night-time can also negatively impact plant photosynthesis through increasing autotrophic respiration (Peng et al., 2013). A field warming experiment at a temperate dry grassland site in China showed that nighttime warming stimulated plant photosynthesis by about 20% (Wan et al., 2009). This observation was supported by the analysis of Peng et al. (2013), who reported a general positive correlation between growing season T_{min} and NDVI across the temperate dry regions. The increased metabolic use of leaf carbohydrates at night (Turnbull et al., 2002, 2004) could be mainly responsible for a compensation effect leading to enhanced vegetation photosynthetic activity in these regions (Wan et al., 2009). The results of this study, however, showed that the positive correlation between T_{min} and NDVI is mainly evident in spring and summer (Fig. 1), implying that the dominant ecophysiological effects of nighttime warming vary seasonally. In most of central and western Asia, for example, a significantly positive correlation between T_{min} and NDVI was observed during spring and summer, but autumn NDVI show significant negative correlation with autumn T_{min}.

Similar to the temperate zone, the direction and the strength of the T_{min}-NDVI relationship in high latitudes shows strong seasonal variability. Opposite to the common speculation in the literature that global warming could enhance vegetation photosynthetic activity in the Northern Hemisphere (Keeling et al., 1996; Myneni et al., 1997; Zhou et al., 2001; Peng et al., 2011), the study of Peng et al. (2013) pointed out that rising T_{min} was associated with reduced vegetation productivity in cold and wet regions. Here, we found that in the high latitude cold regions, a negative correlation between T_{min} and NDVI is more common during autumn than during spring and summer, indicating that autumn is the main contributing season to the negative response of growing season averaged NDVI to increases in growing season averaged T_{min}, as reported by Peng et al. (2013). The colder and longer nights in autumn may be part of the explanation, but further studies are needed to explore the underlying mechanisms.

Prior research indicated that increase in maximum temperature could enhance rice yields in tropical and subtropical Asia (Welch et al., 2010). Here we also observed a positive effect of T_{max} on spring NDVI in some regions dominated by crops, such as central North American. However, a negative effect of T_{max} on summer and autumn NDVI is also observed in those areas, likely due to heat induced chloroplast damage, spikelet sterility, higher respiration demand and greater evaporative loss (Wassmann et al., 2009, Dhakwa & Cambell 1998). The effect of T_{min} on cropland NDVI is also very complicated. On one side, increased T_{min} could reduce crop growth through increasing respiration losses, reducing grain-filling duration and endosperm cell size (Welch et al., 2010). On the other side, increased T_{min} could benefit crop growth through reducing the occurrence frequency of frost events (Lobell DB et al., 2007). Thus the apparent response of crop growth to T_{min} is the balanced result of those two opposite impacts. Additionally, it should be noted that cropland NDVI is also regulated by agricultural management, like reaping and irrigating.

Land surface models are used to project future states of ecosystems and climate. We show here that current land surface models cannot capture the seasonal variation in the response of photosynthetic activity to daytime and night-time temperature changes across the Northern Hemisphere. This may provide some new insights on understanding the uncertainties in current IPCC AR5 model projections of future changes in global carbon cycle and its feedback to climate (IPCC, 2013). It is not clear, however, if this inconsistency between satellite data analysis and modeled GPP analysis is induced by bias of climate forcing from CRU-NCEP (with 6 hour temporal resolution) or in modeled vegetation productivity due to the inaccurate representation of physical process (such as soil moisture) or the missing ecophysiological process (e.g., the response of plant photosynthesis to nighttime warming through altered draw-down of leaf carbohydrates at night) in the models. In addition to the direct impacts on plant photosynthesis and respiration, warming could also profoundly alter plant community structure and composition (Wu et al., 2012; Peñuelas et al., 2013), which has also important implications for ecosystem productivity (Wang et al., 2012; Liu et al., 2013). Such warming-induced changes in plant community structure and composition may play a more important role in regulating the response of vegetation productivity to temperature change in grasslands than in forests. One can expect that the structurally changed plant community may bring further changes in the seasonal variability of the vegetation photosynthetic activity response to temperature change, given the differences in phenology among different vegetation types.

In summary, we here show differences in vegetation activity correlations to diurnal temperature changes across different seasons and regions in the Northern Hemisphere. Our results suggest that the diurnal and seasonal variations in vegetation responses to temperature changes are important for understanding the changes in vegetation photosynthetic activity in a warming world. Such diurnal and seasonal variations, however, have rarely been incorporated in current experimental and modelling studies on vegetation responses to global warming which are overwhelmingly based on daily or growing season mean air temperature. New field warming experiments with differently elevated temperature during day versus night, and across different seasons, are urgently needed. Such experiments will shed new light on the ecophysiological effects of daytime and night-time warming during different seasons, and can be used to improve the performance of current land surface models.

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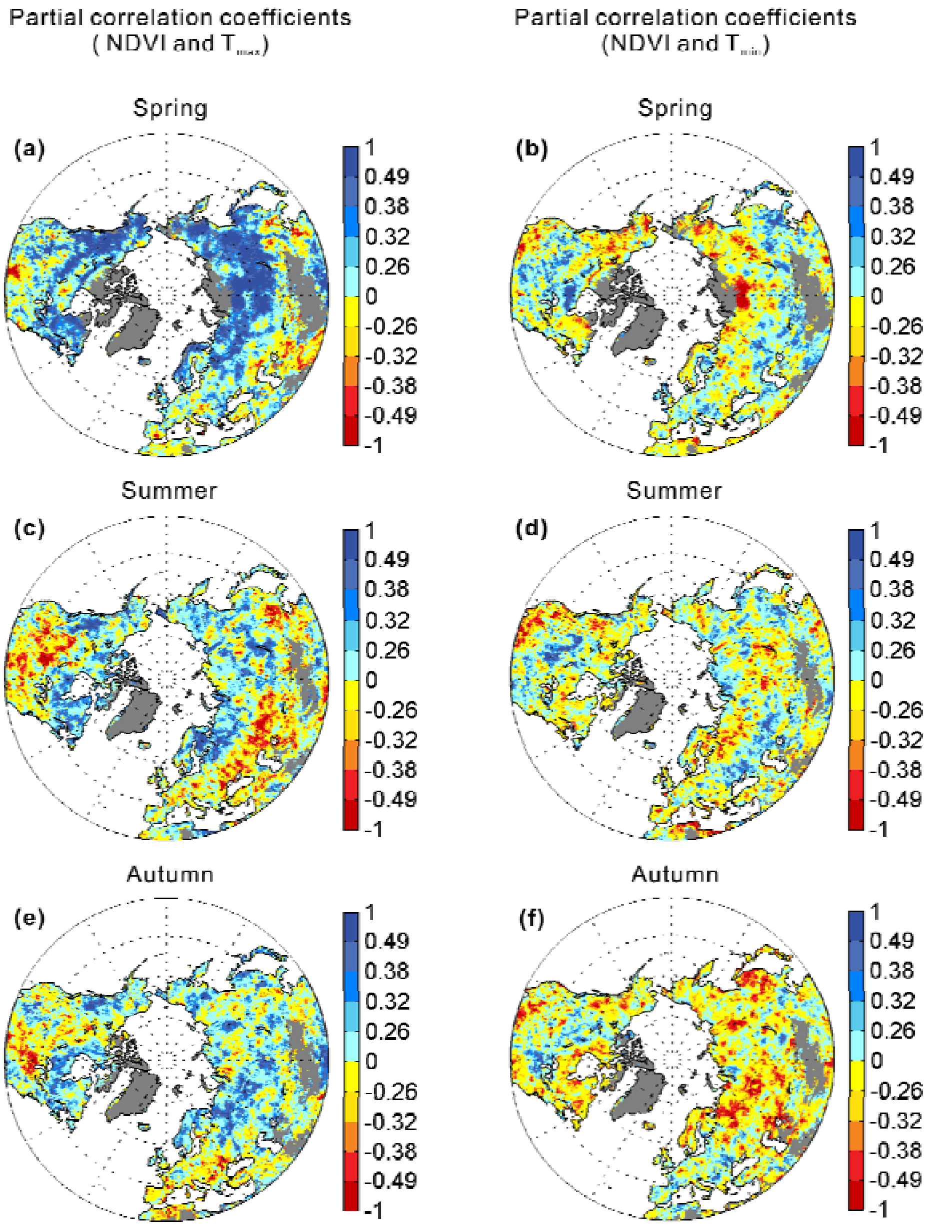
Figure legends

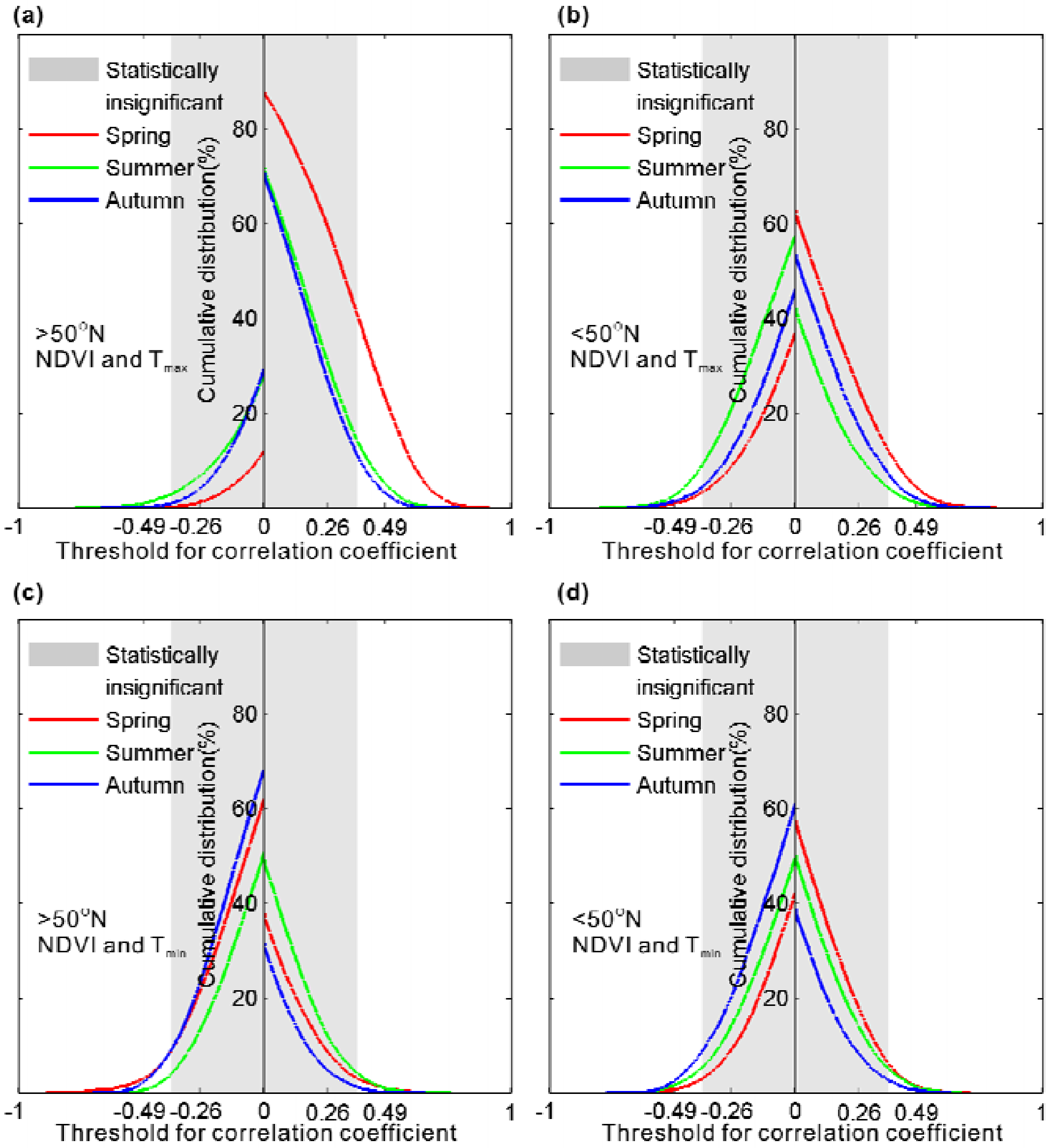
Figure 1 Spatial patterns of the correlation between seasonal NDVI and corresponding daily maximum (T_{max}) or minimum temperatures (T_{min}) in the mid- and high- latitudes of the Northern Hemisphere during 1982-2011. (a), (c) and (e) are the spatial patterns of partial correlation coefficients between NDVI and T_{max} during April-May (a), June-August (c) and September-October (e), respectively. The corresponding T_{min}, precipitation and solar radiation are controlled for in the calculation. (b), (d) and (f) show the partial correlation coefficients between NDVI and T_{min} during April-May (b), June-August (d) and September-October (f), while T_{max}, precipitation and solar radiation are controlled for. The segment points ±0.49, ±0.38, ±0.32 and ±0.26 correspond to 1%, 5%, 10% and 20% significant level of student's t-test.

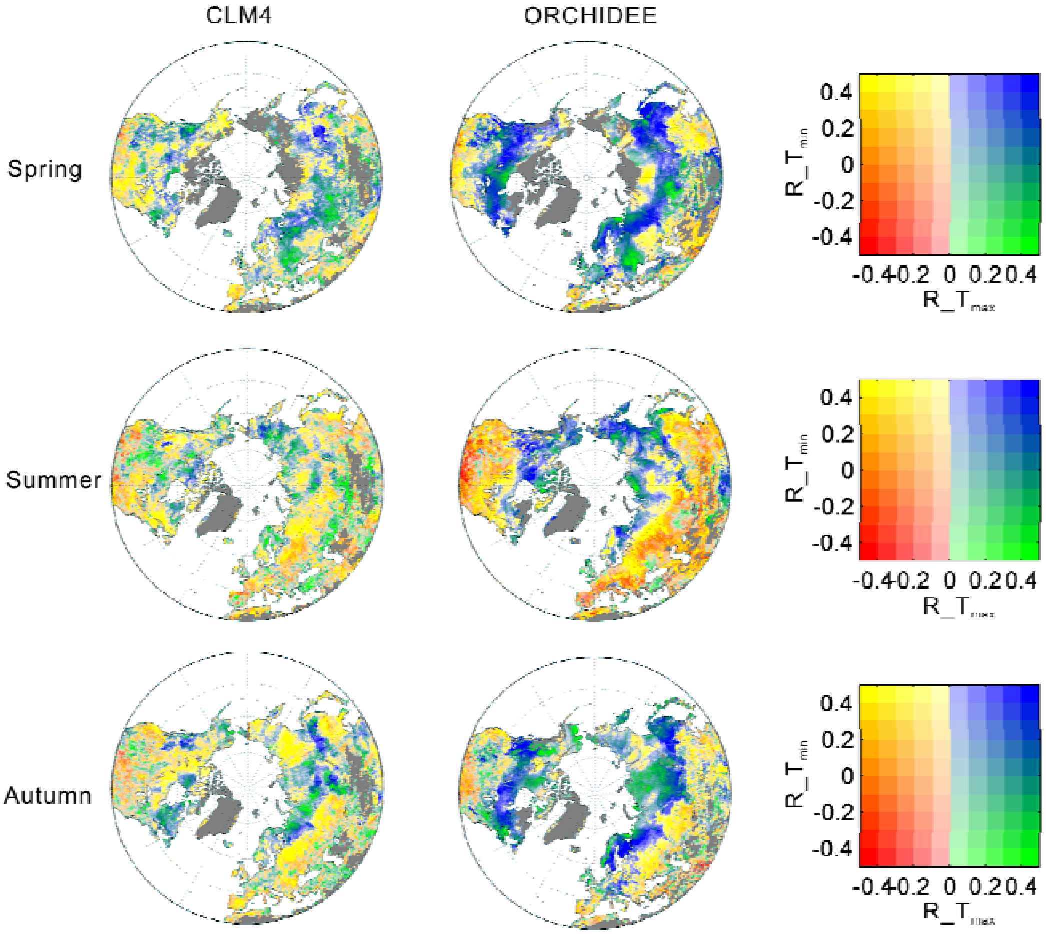
Figure 2 Cumulative frequency distributions of the partial correlation between seasonal NDVI and daily maximum (T_{max}) or minimum temperatures (T_{min}). (a)-(b) are the cumulative frequency distributions of the partial coefficients between spring (April-May, red lines), summer (June-August, green lines) and autumn (September-October, blue lines) NDVI and T_{max} in boreal zone (a) and temperate regions (b), respectively. (c)-(d) show the cumulative frequency distributions of the partial coefficients between seasonal NDVI and T_{min} in boreal zone and temperate regions. The cumulative distributions of positive and negative correlations are calculated separately. For positive correlations (right part of each subfigure), the frequency is cumulated from +1 while for negative correlations (left part of each subfigure), the frequency is cumulated from -1.

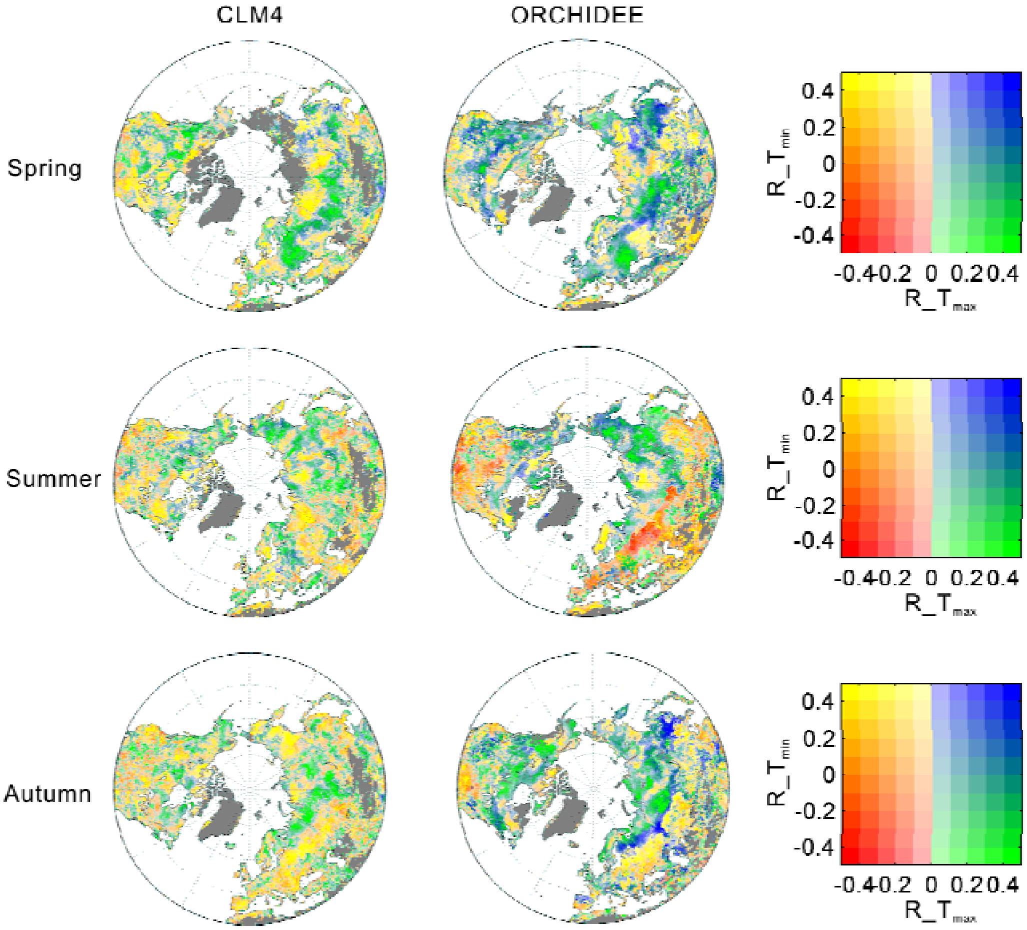
Figure 3 The responses of model simulated GPP to daily maximum temperature (T_{max}) or minimum temperature (T_{min}) in the mid- and high- latitudes of the Northern Hemisphere during 1982-2010. The color-coded patterns are derived from a two-dimensional color map in which the horizontal gradient represents the variations of partial correlation coefficients between GPP and T_{max}, and the vertical gradient corresponds to the variations in the partial correlation coefficients between GPP and T_{min}.

Figure 4 The responses of model simulated LAI to daily maximum temperature (T_{max}) or minimum temperature (T_{min}) in the mid- and high- latitudes of the Northern Hemisphere during 1982-2010. The color-coded patterns are derived from a two-dimensional color map in which the horizontal gradient represents the variations of partial correlation coefficients between LAI and T_{max}, and the vertical gradient corresponds to the variations in the partial correlation coefficients between LAI and T_{min}.


Partial correlation coefficients
(NDVI and T_max)
Partial correlation coefficients
(NDVI and T_min)
Spring
(a)
(b)
Summer
(c)
(d)
Autumn
(e)
(f)
1
0.49
0.38
0.32
0.26
0
-0.26
-0.32
-0.38
-0.49
-1


(a)
(b)
(c)
(d)
Statistically insignificant
Spring
Summer
Autumn
>50°N
NDVI and T_{max}
<50°N
NDVI and T_{max}
>50°N
NDVI and T_{min}
<50°N
NDVI and T_{min}
Cumulative distribution(%)
20
40
60
80
-1
-0.49
-0.26
0
0.26
0.49
1
Threshold for correlation coefficient


CLM4
ORCHIDEE
Spring
Summer
Autumn
R_T_{min}
0.4
0.2
0
-0.2
-0.4
-0.4-0.2 0 0.2 0.4
R_T_{max}
R_T_{min}
0.4
0.2
0
-0.2
-0.4
-0.4-0.2 0 0.2 0.4
R_T_{max}
R_T_{min}
0.4
0.2
0
-0.2
-0.4
-0.4-0.2 0 0.2 0.4
R_T_{max}


CLM4
ORCHIDEE
Spring
Summer
Autumn
R_T_{min}
0.4
0.2
0
-0.2
-0.4
-0.4-0.2 0 0.2 0.4
R_T_{max}