Key Points:

- The temperature sensitivity of photosynthesis significantly declined during the last two decades
- The nonlinear thermal responses of photosynthesis was the main driver of the attenuated positive effect of warming
- The temperature-limited northern ecosystems may be approaching the temperature tipping point

Nonlinear Thermal Responses Outweigh Water Limitation in the Attenuated Effect of Climatic Warming on Photosynthesis in Northern Ecosystems

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Abstract Plant photosynthesis is strongly limited by temperature at high northern latitudes. The temperature sensitivity of plant photosynthesis in scenarios of future climatic warming, however, is highly uncertain. We used sun-induced fluorescence—a satellite proxy for plant photosynthesis—to analyze the spatiotemporal response of photosynthesis to temperature at high northern latitudes. We detected a widespread decline in the sensitivity of photosynthesis to temperature during the last two decades: 3.25 versus 2.19%/°C, in the 2000s and 2010s, respectively. We used methods of machine learning and temporal composition to characterize the contribution of nonlinear thermal responses and water limitation. Both methods consistently identified the nonlinear thermal responses as the main driver of the attenuated positive warming effect. We highlighted the traditionally temperature-limited ecosystems at high northern latitudes may be approaching the temperature tipping point, beyond which the warming effect on plant photosynthesis would transition from positive to negative.

Plain Language Summary Terrestrial plants absorb atmospheric carbon dioxide (CO_2) by photosynthesis, which is a major mechanism mitigating climate change. Plant photosynthesis is strongly limited by temperature at high northern latitudes. Climate warming has decreased the temperature limitation on plant photosynthesis, and induced an increase in photosynthesis. Recent studies revealed a decline in the sensitivity of photosynthesis to temperature with ongoing warming. However, the underlying mechanism is still not clear. We used satellite-observed sun-induced fluorescence data to analyze the spatiotemporal response of photosynthesis to temperature at high northern latitudes. We confirmed the widespread decline in the temperature sensitivity of photosynthesis during the last two decades: 3.25 versus 2.19%/°C, in the 2000s and 2010s, respectively. We further provide compelling empirical evidence that the nonlinear thermal responses (direct effect of warming) outweighed water limitation (indirect effect of warming), accounting for this attenuated effect. We suggested that ecosystems at high northern latitudes are approaching the margin of the benefit of climatic warming.

1. Introduction

Terrestrial plants absorb carbon dioxide (CO_2) from the atmosphere by photosynthesis, which is a major mechanism that offsets anthropogenic carbon emissions and mitigates climate change (Anav et al., 2015; Keeling et al., 1996; Running, 2012). Temperature plays a critical role in controlling plant photosynthetic activity and is therefore one of the main determinants of the global carbon balance (Berry & Bjorkman, 1980; Jung et al., 2017). Anthropogenic climatic warming has decreased the limitation of temperature on plant photosynthesis, especially in high-latitude ecosystems (Huang et al., 2019; Keenan & Riley, 2018), and has exerted positive effects on photosynthesis, indicated by the widely reported global greening (C. Chen et al., 2019; Lucht et al., 2002; Myneni et al., 1997; Piao et al., 2020; Zhu et al., 2016). This warming-induced increase in photosynthesis has further provided a negative feedback to global warming (Zeng et al., 2017).

Anthropogenic warming will continue in the future, but the corresponding response of plant photosynthesis to increasing temperatures is highly uncertain. Several recent studies reported that the greening trends have stalled or even reversed (Berner et al., 2020; Pan et al., 2018; Yuan et al., 2019; A. Z. Zhang et al., 2021). Analyses of the correlation between temperature and photosynthesis, represented by several indicators including satellite-recorded greenness, tree-ring and atmospheric CO_2 measurements, have also indicated weakening

positive or emerging negative relationships (D'Arrigo et al., 2004; Piao et al., 2017; Piao et al., 2014; Wang et al., 2018). These multiple lines of evidence together suggest an attenuated sensitivity of plant photosynthesis to temperature, that is, the magnitude of photosynthetic responses per °C, due to global warming.

Our limited understanding about the effect of warming on plant photosynthesis leads to large uncertainties in comprehending carbon-climate feedbacks and climatic projections (Friedlingstein et al., 2014; Hu et al., 2021). Two main non-exclusive hypotheses may account for the smaller effect of climatic warming on plant photosynthesis: (a) the hypothesis of nonlinear thermal responses, where photosynthetic activity responds parabolically to temperature, that is, photosynthesis first increases with temperature when the ambient temperature is below the optimal temperature, and this increase decelerates and then reverses when the ambient temperature approaches and surpasses the optimum temperature, because electron transport and Rubisco enzymatic capacities become impaired (Berry & Bjorkman, 1980; Huang et al., 2019; Yamori et al., 2014), and (b) the hypothesis of water limitation, where climate warming will incur an exponential increase in the vapor-pressure deficit (VPD) and then cause water stress, because the increased VPD generally causes more atmospheric demand than input from precipitation (Grossiord et al., 2020; Sherwood & Fu, 2014). The photosynthetic rate would decrease under drought conditions due to stomatal closure to prevent hydraulic failure (McDowell et al., 2011).

Elucidating the roles of these two main hypotheses in the attenuated effect of warming has important implications for the accurate projection of carbon uptake. If water limitation dominated the observed attenuated effect of warming, high northern ecosystems may still benefit the most from future warming, because the effect of warming-induced dryness could be partially mitigated by an increased water-use efficiency if the effect of CO_2 fertilization was sustainable (De Kauwe et al., 2021; Smith et al., 2020). In contrast, if the hypothesis of nonlinear thermal responses prevailed, the attenuation of the effect of a positive photosynthetic response would accelerate, and regions exhibiting negative responses to warming may expand substantially, because the thermal adaptation of plant photosynthesis is much slower than the ongoing rate of warming (A. P. Chen et al., 2021; Duffy et al., 2021).

We aimed to characterize the contribution of nonlinear thermal responses and water limitation to the attenuated effect of warming on photosynthesis in high northern ecosystems. We used the clear-sky sun-induced fluorescence (SIF) of the contiguous SIF (CSIF) data set as a proxy of plant photosynthesis, which was strongly correlated with ecosystem gross primary productivity (GPP) (Y. Zhang et al., 2018). The aridity index, calculated as the ratio of precipitation to potential evapotranspiration both from the ERA5 data set (Hersbach et al., 2020), was used to represent water limitation. The aridity index characterizes the dryness in terms of the ecological water balance, accounting for both water supply and demand. The apparent temperature sensitivity (St), expressed as the slope of the linear regression between SIF and air temperature, was used to represent the effect of warming on plant photosynthesis.

2. Materials and Methods

2.1. Sun-Induced Chlorophyll Fluorescence Dataset

SIF is an electromagnetic signal emitted by chlorophyll molecules after the absorption of solar radiation (Porcar-Castell et al., 2014). SIF has been widely used as a proxy of GPP due to its physiological link to plant photosynthesis (Zarco-Tejada et al., 2013). We used SIF rather than existing satellite GPP products (e.g., MODIS, FluxCom) because this data driven approach avoids the uncertainties associated with the parametrization and calibration of more elaborated GPP models (Y. Zhang et al., 2018). We used clear-sky contiguous SIF (CSIF), with 4-day temporal and 0.05° spatial resolutions, to represent plant photosynthetic activity. CSIF data were generated by a machine-learning method using MCD43C1 C6 reflectance as inputs (Y. Zhang et al., 2018). The machine-learning algorithms were trained over the OCO-2 SIF observations with colocation nadir bi-directional reflectance distribution function adjusted reflectance. We selected clear-sky, rather than all-sky, CSIF since it has a stronger correlation with the original OCO-2 SIF retrievals, and also a stronger correlation with GPP estimates from eddy covariance flux towers (Y. Zhang et al., 2018).

2.2. ERA5 Dataset

We analyzed the $0.1° \times 0.1°$ ERA5 data set to understand the contributions of nonlinear thermal responses and water limitation to the lower temperature sensitivity. ERA5 is the fifth generation of reanalysis produced by the European Center for Medium-Range Weather Forecasts (Hersbach et al., 2020). We extracted daily meteorological data from the original products with hourly resolutions, with a maximized method for air temperature 2 m above the surface and an accumulated method for precipitation and potential evaporation. The aridity index was calculated as the ratio of precipitation to potential evapotranspiration, both accumulated during the growing season. The index defines water limitation in terms of water balance. High and low values represent wet and arid scenarios, respectively.

We selected aridity index because indicators defined in terms of water balance are suitable to quantify the effects of water limitation on GPP variations (Gampe et al., 2021; Jiao et al., 2021). Several recent papers highlighted the importance of VPD on land carbon dynamics (Grossiord et al., 2020; Lu et al., 2022; Yuan et al., 2019). However, Liu et al. (2020) observed VPD plays a secondary role, than soil moisture, in restraining plant growth. This topic is still highly debated and out of the scope of this study.

2.3. MCD12C Land-Cover Dataset

We focused on natural vegetation to eliminate the influence of human management. The 0.05° MODIS land-cover Collection 6 (MCD12C) with International Geosphere Biosphere Programmed classes (Friedl et al., 2010) was used to exclude croplands from the analysis (see Figure S1 in Supporting Information S1).

2.4. Data Analysis

Our aim was to examine the changes in the sensitivity of plant photosynthesis to temperature across ecosystems at high northern latitudes (>50°N). The 20-year study period, from 2000 to 2019, represents the maximum temporal overlaps of the CSIF and ERA5 data sets. We harmonized all data sets to a 0.1° latitude-longitude resolution, following the ERA5 grid, to ensure consistency among them. Average values were used for CSIF, and the dominant class was used for MCD12C.

The sensitivity of photosynthesis to temperature was calculated over the growing season. We obtained the growing season for each pixel by first smoothing the original CSIF time series using Savitzky-Golay filtering (J. Chen et al., 2004) and then linearly interpolating the series to daily frequency. The smoothed daily time series was then linearly normalized to [0, 1], and the start and end of the growing season (SOS and EOS) were defined as the dates passing through the dynamic threshold of 20% of the annual amplitude. The yearly SOS and EOS were averaged over 2000–2019 to provide the climatological values for these phenological metrics (see Figure S2 in Supporting Information S1). The apparent temperature sensitivity (St) of photosynthesis was defined as the slope of the linear regression between SIF and temperature, both aggregated over the climatological growing season. For a better comparison, St was normalized by the multi-year averaged growing season SIF. St therefore indicated the change in SIF (in %) per degree warming.

A machine-learning method was developed to identify the contributions of nonlinear thermal responses and water limitation to the lower St. Specifically, a random forest (RF) model with 500 decision trees was trained to learn the transfer relationship from temperature and the aridity index to St. The training data set was composed of St calculated over 2000–2019, and temperature and the aridity index were both averaged over 2000–2019. We applied this trained RF model to the two decades in our study (2000–2009 vs. 2010–2019, referred as $St^{2000\text{-}2009}$ and $St^{2010\text{-}2019}$, respectively) with corresponding decadal averaged temperature and aridity index as inputs. The results indicated that the trained RF model could successfully reproduce the observed St (see Figure S3 in Supporting Information S1). Two additional versions of St for 2010–2019 were predicted, one with an actual aridity index during 2010–2019, controlling temperature in the case of 2000–2009 ($St_{AI}^{2010\text{-}2019}$), and the other with actual temperature, controlling the aridity index for 2000–2009 ($St_T^{2010\text{-}2019}$). Finally, we subtracted $St_T^{2010\text{-}2019}$ and $St_{AI}^{2010\text{-}2019}$ from $St^{2000\text{-}2009}$ to obtain the contributions of nonlinear thermal responses and water limitation, respectively, to the inter-decadal decrease in St.

A temporally composite analysis was also used for empirical attribution. For characterizing the influence of nonlinear thermal responses of plant photosynthesis, we sorted the years during 2000–2019 based on the 2-m air
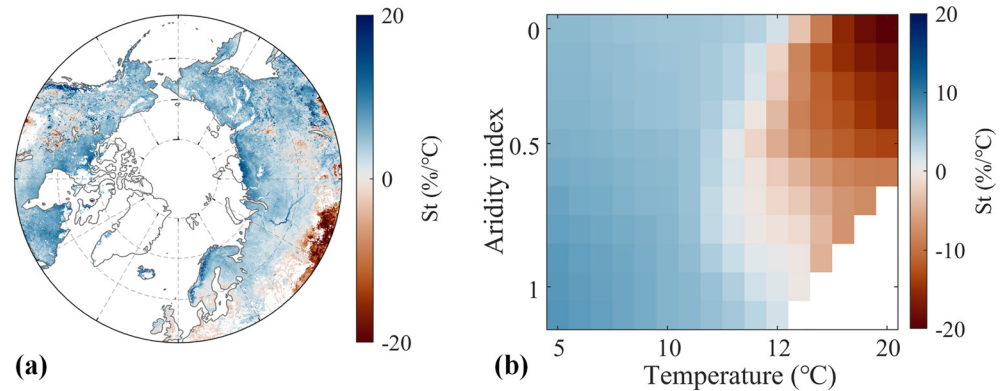
Figure 1. Distribution of the temperature sensitivity of photosynthesis (St). St was calculated as the slope of the linear regression between sun-induced fluorescence (SIF) and air temperature (both averaged over the growing season) during 2000–2019. (a) Spatial distribution of St at high northern latitudes (>50°N). (b) St in the temperature-aridity space. Each climatic bin is defined by 1°C intervals of temperature and 0.1 intervals of the aridity index. The temperature and aridity index were both averaged over the growing seasons from 2000 to 2019 to represent the background climatic conditions.

temperature for each grid and identified the 10 years with the highest temperatures as warm years and the other 10 years as cold years. We then separately calculated St for the warm and cold years. The difference between them was used to characterize the variation in St induced by nonlinear thermal responses. We also used a similar procedure to characterize the influence of water limitation, with the aridity index used to identify wet and dry years.

The optimum temperature was also extracted to compare it with ambient temperature. CSIF time series throughout the entire monitoring period and the corresponding temperature were grouped into 1°C temperature bins for each pixel. The 90% quantile of the CSIF data was used as the response of SIF within each temperature bin, and the running means of every three temperature bins were then calculated to develop the temperature response curve of SIF (Huang et al., 2019). The optimum temperature was identified from the response curve at which SIF was maximized. Details regarding the optimum temperature calculation can be found in Huang et al. (2019). The spatial distributions of optimum temperature and the difference relative to the growing season averaged temperature for 2000–2009 and 2010–2019 were shown in Figure S4 in Supporting Information S1.

3. Results

St during 2000–2019 averaged 3.20 ± 5.61%/°C (mean ± σ) across the study area (>50°N). We observed a latitudinal gradient, with a negative response mostly along the southern boundary of the study area: western and central Europe, and western Siberia (Figure 1a). St was highest mainly in the Arctic, where the growing-season temperature was lowest (see Figures S5a and S5b in Supporting Information S1). The cut-off latitude between the negative and positive responses was about 53°N (Figure 2d). Putting St in a temperature-aridity space identified a gradient of St along the temperature variation across all values of the aridity index (Figure 1b). The impact of the aridity index on St was weaker than the impact of temperature, but aridity index regulated the response of St to temperature. The stronger gradient with temperature than the aridity index suggested that the direct effect of warming (nonlinear thermal responses) outweighed the indirect effect (water limitation) in the attenuated response of photosynthesis in northern ecosystems to climatic warming.

The spatial distributions of St were very similar during the last two decades (see Figures 2a and 2b), but their magnitudes differed significantly: 3.25 ± 6.41%/°C for 2000–2009 versus 2.19 ± 6.20%/°C for 2010–2019 (t-test, P < 0.0001). We mapped their difference and observed a widespread decrease in St in the last decade (Figure 2c). The most notable decreases were in eastern Europe and eastern Siberia, where they were accompanied by concordant increases in both temperature and aridity (see Figures S5c and S5f in Supporting Information S1). Note the net ecosystem productivity is also controlled by respiration which increases exponentially with warming. Therefore, the attenuation of the positive effects of warming on net carbon uptake may be greater than revealed here.
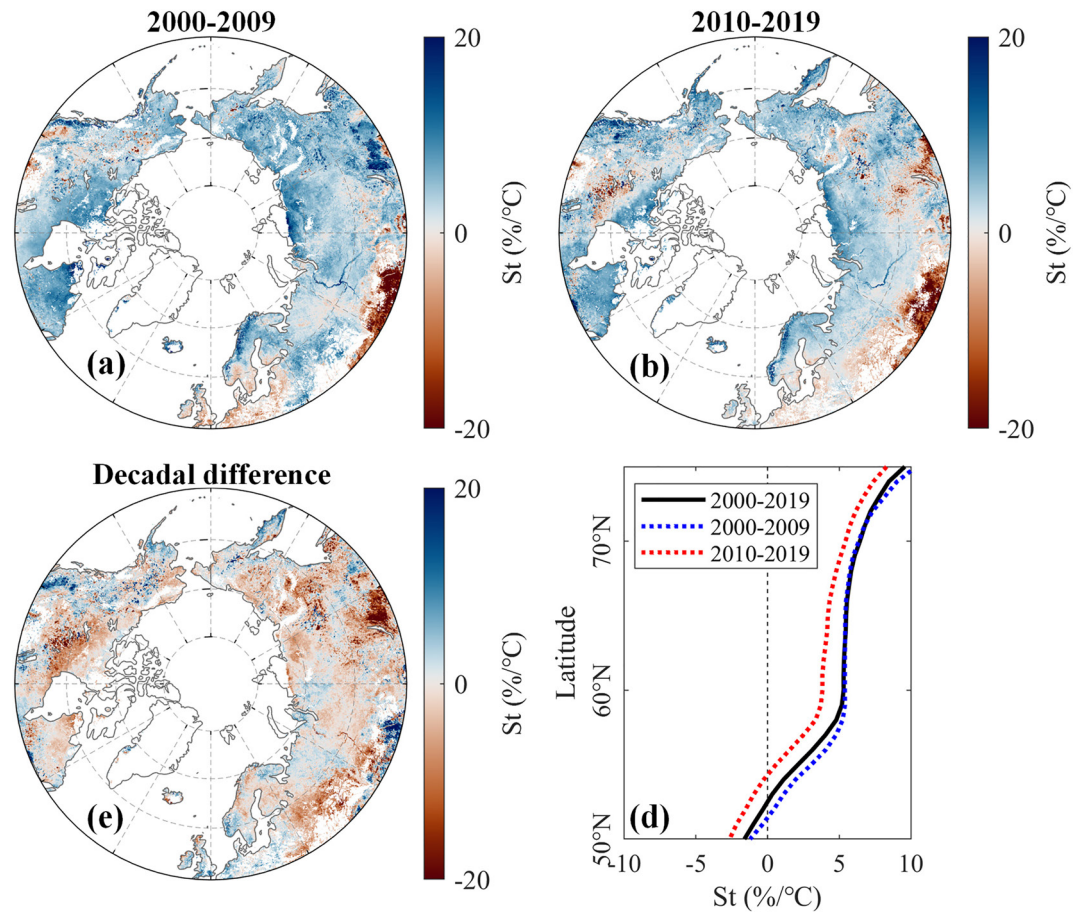
Figure 2. Decreased temperature sensitivity (St) of photosynthesis at high northern latitudes (>50°N) during the last two decades (from 2000–2009 to 2010–2019). St was calculated as the slope of the linear regression between sun-induced fluorescence (SIF) and temperature (both averaged over the growing season). Spatial distributions of St for (a) 2000–2009, (b) 2010–2019, and (c) their difference. (d) Average St values by latitude during 2000–2009, 2010–2019, and 2000–2019.

Interestingly, we detected many areas, mainly along the southern boundary of our study area, where St reversed its direction from positive to negative, for example, eastern Europe, western and southern Siberia, and central Canada. The reversal of the direction of response caused a 3° northward shift of the areas benefiting from warming (with positive responses to warming), from 52°N to 55°N (Figure 2d).

We calculated the contributions of nonlinear thermal responses and water limitation to the decreased St using a machine-learning method. The widespread warming and drying trends (see Figures S5c and S5f in Supporting Information S1) make these two factors both negative drivers of the inter-decadal variation in St (Figure 3). The contribution from nonlinear thermal responses was an order of magnitude higher than that from water limitation (−1.05% vs. −0.10%) throughout the high northern latitudes. The influence of water limitation on the decrease in St was generally in grasslands in western Siberia and northeastern Canada, which are sensitive to disturbances in water availability because of their shallow root systems, and exhibited a drying trend during the last decade (see Figure S5f in Supporting Information S1). In comparison, nonlinear thermal responses prominently reduced St, especially in the southern (50°N) and northern (the Arctic regions) boundaries in our study area: the ecosystems near 50°N are close to their optimum temperatures (Liu, 2020), so climatic warming would definitely reduce St regardless of the specific rate (see Figure S4 in Supporting Information S1). The effect of Arctic amplification substantially increased the ambient temperature of plant photosynthesis (see Figure S5c in Supporting Information S1), although it is generally regarded as far below the optimum (Liu, 2020).

The differences in composite decadal St (see Section 2) over contrasting dryness (2.87 ± 6.36%/°C for dry years vs. 4.36 ± 5.51%/°C for wet years, Figures 4a and 4b) and warmth (1.56 ± 9.29%/°C for warm years vs.
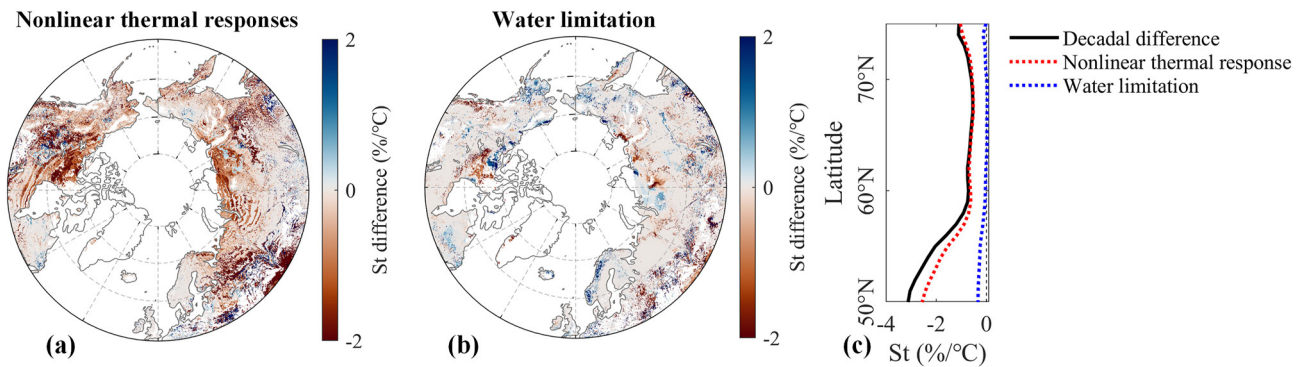
Figure 3. Inter-decadal difference (2010–2019 vs. 2000–2009) in temperature sensitivity (St) caused by direct (nonlinear thermal responses) and indirect (water limitation) effects of warming. Inter-decadal differences in St from (a) nonlinear thermal responses and (b) water limitation. (c) Latitudinal distributions of inter-decadal differences in St and those caused by nonlinear thermal responses and water limitation. The contributions of the two effects were identified using a machine-learning method.

$3.92 \pm 8.11\%/°C$ for cold years, Figures 4d and 4e) were $-1.49 \pm 6.70\%/°C$ and $-2.37 \pm 9.29\%/°C$, respectively, supporting the stronger contribution of nonlinear thermal responses than water limitation to the decrease in St. The latitudinal distributions of St (See Figures 4c and 4f) indicated that productivity would increase at all latitudes in our study area due to climatic warming if the ambient environment was wet and/or cold. In contrast, the southern boundary of the areas benefiting from warming would retreat to 54°N and 56°N in dry and warm years, respectively.
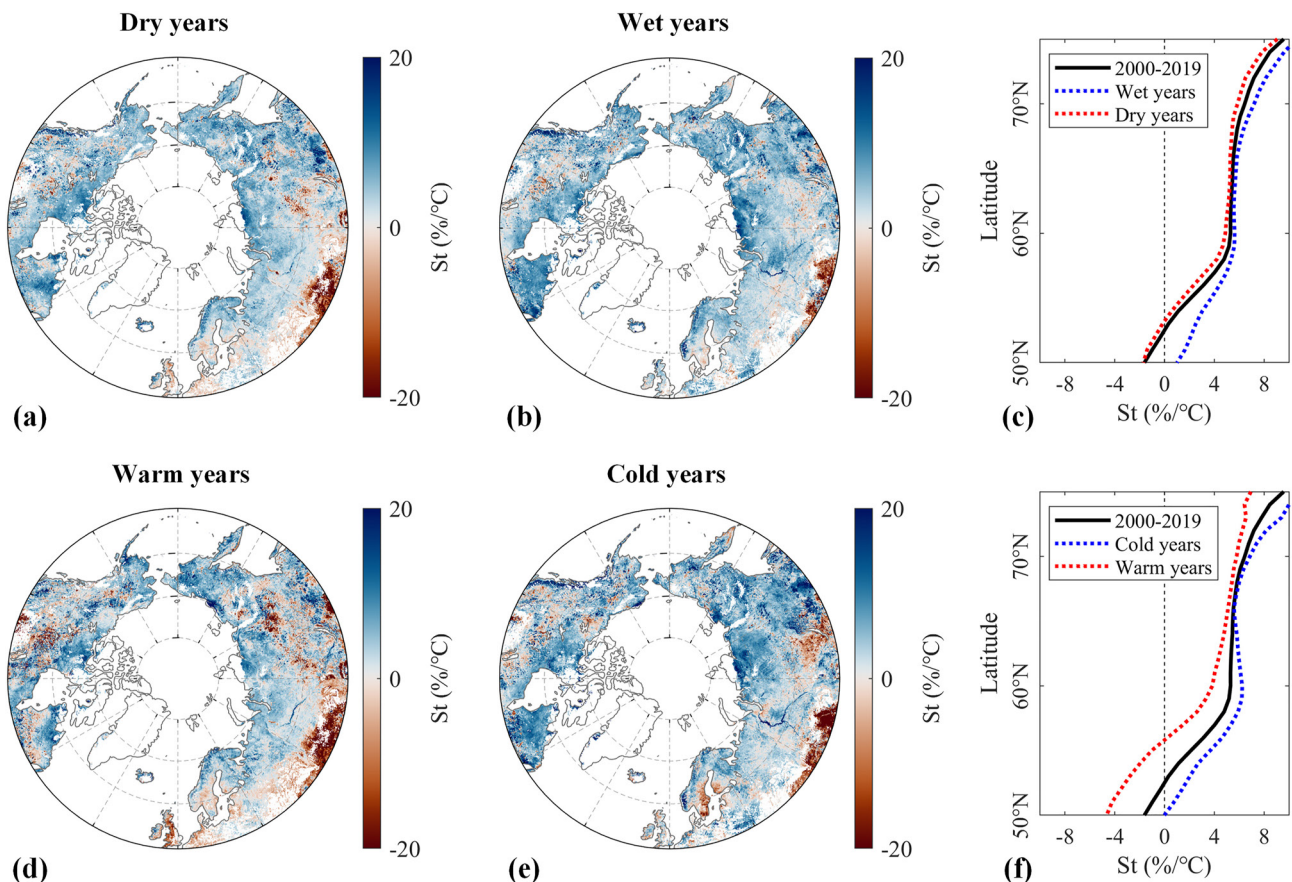

Figure 4. Temperature sensitivity (St) of photosynthesis in contrasting scenarios of aridity and warmth. Composite patterns of St for the 10 (a) driest and (b) wettest years and (c) their values averaged by latitude. Composite patterns of St for the 10 (d) warmest and (e) coldest years and (f) their values averaged by latitude.

4. Conclusions

Ecosystems at high northern latitudes are limited by temperature, and climatic warming favors vegetation productivity (Keenan & Riley, 2018). We used satellite-observed SIF data to detect the effect of a widespread decrease in temperature sensitivity on photosynthesis in northern ecosystems during the last two decades. We further provide compelling empirical evidence that the nonlinear thermal responses (direct effect of warming) outweighed water limitation (indirect effect of warming), accounting for this attenuated effect. Our study highlights the necessity of current land-surface models to accurately reproduce the sensitivity of photosynthesis to temperature. The thermal adoption of plant photosynthesis at the ecosystem scale is slow and may not even occur (A. P. Chen et al., 2021; Duffy et al., 2021; Huang et al., 2019), so ecosystems at high northern latitudes are approaching the margin of the benefit of climatic warming. Many other factors, for example, nutrient limitation, wild fire, and climatic extremes (Angert et al., 2005; Goetz et al., 2005; Penuelas et al., 2017), may further accelerate the reduction of the beneficial role of climatic warming on plant photosynthesis. Therefore, the temperature tipping point at which future warming would exert a negative role on plant photosynthesis may come earlier than previously expected.

Data Availability Statement

The CSIF data are available at https://osf.io/8xqy6/, the ERA5 data are available at https://cds.climate.copernicus.eu/cdsapp%23%21/dataset/reanalysis%2Dera5%2Dland%3Ftab%3Dform, and the MCD12C data are available at https://lpdaac.usgs.gov/products/mcd12c1v006/.

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