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Light limitation regulates the response of autumn terrestrial carbon uptake to warming

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Global warming is projected to shift the phenology and increase the productivity of northern ecosystems¹⁻⁶. Both changes will further feed back to climate through biophysical and biogeochemical processes and are critical for future prediction^{7,8}. However, it remains unclear whether warming and the extended growing season, especially in autumn, would lead to increased net ecosystem carbon uptake^{9,10}. Here we analyse satellite observations, field measurements and model simulations and show a prevalent radiation limitation on carbon uptake in northern ecosystems, especially in autumn. By comparing the start and end of the growing season estimated from vegetation indices and from solar-induced chlorophyll fluorescence (a proxy for gross primary production^{11,12} (GPP)), we find a greater change in greenness-based start and end of season than that from GPP, mostly caused by the radiation limitation on photosynthesis. This radiation limitation explains the contrasting responses of autumn net carbon exchanges to warming, using both eddy covariance measurements and model simulations from Coupled Model Intercomparison Project Phase 5. Regions with weak radiation limitation benefit more from warming and enhanced vegetation greenness in autumn, where GPP increases can outweigh the warming-induced respiration carbon losses. With continued warming, radiation limitation will increase and exert a strong upper bound on northern ecosystems to act as carbon sinks.

Temperature is considered the primary abiotic limitation in northern terrestrial ecosystems¹. Higher temperatures in the spring usually lead to an earlier start of the growing season (SOS), higher photosynthetic activity and carbon sequestration^{2,10,13}. However, warming in autumn has confounding effects on carbon uptake in non-water-limited ecosystems, as the extended growing season not only increases plant photosynthesis but also enhances ecosystem respiration⁹. Site-level observations^{10,14} and atmospheric CO₂ measurements9,15 have shown contrasting responses of ecosystem carbon uptake to the warming-induced delay of the end of growing season (EOS), suggesting that these responses might be ecosystem dependent. However, the underlying mechanisms controlling this temperature sensitivity are unclear. The key to tackling this problem is to understand in which case the delayed EOS can lead to increased photosynthesis sufficient to balance the higher carbon loss from respiration.

Here we analyse the trends of SOS and EOS from 2001 to 2017 to understand the effect of changes in plant phenology on regional carbon cycling. To quantify changes in the photosynthetic active period to greenness-based growing season lengths, we use a recent machine-learning-generated solar-induced chlorophyll fluorescence (SIF) dataset¹⁶ to derive gross primary production (GPP)-based SOS and EOS, and compare them with greenness-based SOS and EOS derived from two vegetation indices (VIs). SIF is emitted as a competing pathway of excited chlorophyll^{17,18} and shows a strong correlation with ecosystem GPP (refs. 11,12). Using the machine learning algorithm trained on SIF observations from Orbiting Carbon Observatory-2 (OCO-2), we generated a long-term gridded SIF dataset from spectral reflectance and radiation (contiguous SIF (CSIF)¹⁶; see Methods). The CSIF dataset has low uncertainty, contiguous global coverage and high temporal resolution¹⁶. It well captures the seasonal pattern of the OCO-2 signals and is suitable to be used as a proxy for GPP for phenology retrievals (Extended Data Fig. 1). The SOS and EOS retrieved from CSIF show very high consistency, in terms of both spatial and interannual variability, with those retrieved from Global Ozone Monitoring Experiment-2 (GOME-2) SIF and from GPP estimates from eddy covariance flux towers (Extended Data Figs. 1 and 2).

Using an ensemble of SOS and EOS retrieved from four different methods (Methods and Extended Data Figs. 2 and 3), we show that the advance of SOS and delay of EOS are widespread across most northern ecosystems (north of 30°N) (Fig. 1a,b). Although different methods yield varying absolute phenological dates, the trends of SOS and EOS calculated from each method are consistent with each other (Supplementary Figs. 1 and 2). Delayed SOSs are found mostly in central Eurasia, while advanced EOSs are evident in middle Siberia and southeastern Europe. The greenness-based SOS trends (represented by the normalized difference vegetation index (NDVI) from MODIS) are consistent in sign with those derived from CSIF (Fig. 1), but exhibit a stronger magnitude $(-0.45 \pm 0.09 \,\mathrm{dyr^{-1}}$ for NDVI and $-0.28 \pm 0.07 \, \text{dyr}^{-1}$ for CSIF; mean \pm s.d.; two-tailed Kolmogorov–Smirnov test, P<0.0001; two-tailed paired Wilcoxon test, P < 0.0001). The EOS trends are also generally consistent for most regions, but they differ in the eastern United States¹⁰, western Canada and Alaska. Similarly, the CSIF-derived EOS exhibits much smaller trends than that of the NDVI $(0.43 \pm 0.11 \, \text{dyr}^{-1}$ for NDVI and $0.13 \pm 0.06 \, \text{dyr}^{-1}$ for CSIF; two-tailed Kolmogorov-Smirnov test, P < 0.0001; two-tailed paired Wilcoxon test, P < 0.0001). The differences between CSIF-based trends and greenness-based trends suggest that the plant photosynthetic period does not increase at the same rate as the vegetation greenness-based growing season length. Additionally, this difference is more pronounced in autumn (70.6% of the greenness-based trend) than in spring (38.6%). We also calculated SOS and EOS trends from the enhanced vegetation index (EVI). They show very similar patterns with those of NDVI (Supplementary Fig. 3), and the difference between CSIF and greenness still exists. In addition to these trend differences, we found a stronger decoupling of GPP-based phenological dates from greenness-based ones for the average EOS than for SOS (Extended Data Fig. 2), which is consistent with a previous study¹⁹. These

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Fig. 1 | Trends of spring growth onset and autumn dormancy onset in 2001-2017. a-d, Growth and dormancy onset trends based on NDVI (a,b) and CSIF (c,d) using the median values from four phenology retrieval methods (see Methods). e,f, Frequency distribution of the growth and dormancy onset trends using these two vegetation indicators. The vertical lines represent the average trend values. The thin lines represent the distribution of the trends using the four phenology retrieval methods.

differences can be mostly attributed to radiation, as we elaborate on below.

Radiation plays an important role in linking vegetation greenness to photosynthesis and can be understood using a light-use efficiency (LUE) model²⁰, with GPP expressed as the product of LUE, photosynthetically active radiation (PAR) and fraction of absorbed PAR (fPAR)-with only the latter being related to vegetation greenness. The importance of the changes in PAR relative to the other components (fPAR×LUE) can be used to quantify the radiation limitation on photosynthesis. We propose that the differences between GPP (CSIF)- and greenness (VI)-based SOS and EOS trends are driven primarily by radiation limitations to photosynthesis in these northern ecosystems. We developed an analytical framework to test this hypothesis: with a one-day delay of the greenness-based EOS, the GPP-based EOS would be delayed by γ_{EOS} (usually less than one) days, so that the greenness increase would be partially compensated by a decrease in clear-sky PAR (PAR_{clear-sky}) (Methods and Extended Data Fig. 4). This γ_{EOS} (or γ_{SOS} for spring) represents the sensitivity of GPP-based phenological changes to greenness-based ones (in days per days), and $1 - \gamma$ (between 0 and 1) can be interpreted as the potential radiation limitation on photosynthesis (that is, in the absence of changes in cloud cover). Compared with previous methods that calculate the radiation limitation on the basis of a cloudiness index¹, our method considers the interaction between plants and the environment, and directly focuses on the seasonal cycle of photosynthesis and greenness.

These sensitivity factors calculated using CSIF/PAR_{clear-sky} (fPAR_c. _{SIF}) represent the radiation limitation to the GPP (Methods and Fig. 2a,b). Spring shows a mean radiation limitation of 21.4%, with a stronger limitation in eastern US deciduous forest, European grass-lands and croplands, and boreal evergreen forest, where an earlier SOS can also be observed (Extended Data Fig. 2). In autumn, we find

a much stronger radiation limitation than in spring $(51.1\% \pm 21.9\%)$, two-tailed Wilcoxon test, P < 0.0001). Yet, the autumn radiation limitation in the eastern US, eastern and central Asia, and western Europe is relatively small. These spatial patterns derived from CSIF are also corroborated by the independent GOME-2 SIF dataset and are insensitive to the threshold we used to derive SOS and EOS (Extended Data Figs. 5 and 6). Evergreen ecosystems tend to have stronger radiation limitations since the relative changes in radiation compared with other factors (greenness and other limitations) are greater than in deciduous ecosystems (Extended Data Fig. 4d). We also find increases in the radiation limitation for both spring and autumn in 2001-2017 (Extended Data Fig. 7), which may be related to the warming-induced extension of the growing season length (Methods and Extended Data Fig. 8). Using NDVI as a proxy for fPAR (fPAR_{NDVI}) instead of fPAR_{CSIP} values of $1 - \gamma$ represent the limitation from both radiation and other environmental factors (Methods and Fig. 2c,d). The spatial patterns of limitation are similar to those estimated from fPAR_{CSIF} but are stronger at high latitudes (north of 50° N), which can be attributed to the additional temperature limitation on photosynthesis. Similarly, the autumn limitation is much stronger than the spring limitation $(67.4\% \pm 22.5\%)$ and $46.8\% \pm 22.4\%$, respectively; two-tailed Wilcoxon test, *P* < 0.0001), but the autumn-spring difference is similar to that estimated from fPAR_{CSIF} (20.6% and 29.8%, respectively). This indicates that radiation is the major abiotic limitation on the photosynthetic period that explains the difference between spring and autumn. These findings using the analytical framework are also consistent with the sensitivities obtained directly from the remote sensing estimates on the basis of the regression slopes between CSIF-based and NDVI-based phenologies (67.6% for autumn and 50.5% for spring) (Fig. 2e,f). These multiple lines of evidence emphasize the key control of light on photosynthesis in autumn, whereas the impact is smaller in the



Fig. 2 | Phenological sensitivity (γ **) between GPP and greenness for spring and autumn. a,b**, Analytical derivation using fPAR_{CSIF}; see Methods, equation (5). **c,d**, Analytical derivation using fPAR_{NDVI}; see Methods, equation (7). **e,f**, Regression slopes between the multimethod ensemble means of CSIF- and NDVI-derived SOS and EOS. The sensitivity factor (γ) represents the extension/shrink of the GPP-based growing season caused by a one-day extension/shrink of the greenness-based growing season. A low value of γ (close to 0 in **a** and **b**) represents strong radiation limitations on GPP-based phenology compared with that from greenness. A high sensitivity represents minimal radiation limitation. The left column is for spring, and the right column is for autumn.

spring¹⁹. This radiation limitation weakens the positive effect of warming on autumn GPP and thus potentially on ecosystem carbon uptake in autumn.

To complement our remote sensing analysis, we analyse 326 site-year eddy covariance (EC) CO_2 measurements from 28 sites in the Tier 1 FLUXNET2015 dataset covering various northern ecosystems. Warming generally extends the photosynthetic active period (Supplementary Fig. 4), together with an increase in GPP and ecosystem respiration for both spring and autumn (Supplementary Fig. 5). However, the net effect is different for spring and autumn. In spring, temperature generally shows a positive effect on net ecosystem exchange (NEE) (Fig. 3a), consistent with results from

atmospheric CO₂ measurements⁹. In autumn, temperature exhibits contrasting effects on NEE (Fig. 3b). A strong correlation can be found between the radiation limitation and temperature sensitivity to autumn NEE (Spearman's $\rho = -0.46$, P = 0.014, Extended Data Fig. 9). Sites with a positive temperature sensitivity to autumn NEE exhibit a significantly greater radiation limitation than those with a negative sensitivity (one-tailed *t*-test, P = 0.003, d.f. = 23.4), emphasizing that sites with a stronger radiation limitation tend to release carbon with warming (and vice versa). The threshold of radiation limitation between positive and negative autumn temperature responses is around $48.2 \pm 7.4\%$.

This radiation regulation on the temperature sensitivity of autumn carbon uptake is also supported by 25 out of 26 Coupled Model Intercomparison Project Phase 5 (CMIP5) models, as demonstrated by a significantly stronger radiation limitation for ecosystems with a positive temperature sensitivity on NEE than those with a negative temperature sensitivity (Extended Data Fig. 10). However, the absolute values of the radiation limitation vary substantially across models, with a majority of models overestimating the threshold (57.1 \pm 7.2%) between negative and positive temperature sensitivity to autumn NEE.

We further compared the latitudinal pattern of radiation limitation from 26 CMIP5 models, grouped by the land models they used with estimates from CSIF as the reference (Fig. 4). There is a large spread across land surface model groups, while the variations within each group are small. In spring, the radiation limitation gradually decreases with latitude (-0.34%) per degree of latitude, P < 0.001, t-test). The smaller radiation limitation in the spring is caused by a lagged temperature and vegetation seasonal cycle compared with radiation. This lagged response also exists along the latitude, causing a reversed latitudinal pattern²¹. Many models can reasonably predict this latitudinal change of radiation limitation, while some models show different patterns or overestimate the rate of change with latitude. For example, the LM3 model used in GFDL-ESM2G and GFDL-ESM2M shows a reversed latitudinal pattern of radiation limitation, which may be caused by a fixed leaf area index at northern high latitudes²². In autumn, we observe an increasing limitation with latitude (0.73% per degree of latitude, P < 0.001, t-test). The stronger radiation limitation at higher latitudes tends to dampen the warming effect on photosynthesis, causing a net carbon loss from ecosystems, while the weaker limitation in low- and mid-latitude temperate forests makes warming more effective in increasing the ecosystem carbon gain. This explains the seemingly contrasting responses of autumn warming to ecosystem carbon fluxes, observed in some recent studies focusing on different regions^{9,10,14,23}. The models exhibit a large spread (~30%) of this radiation limitation across latitudes, because of the large variations in EOS across models (Methods and Supplementary Fig. 6). Yet, the response is relatively well captured by the ensemble mean, allowing us to use these model averages for the prediction of future changes in light limitation.

Using the CMIP5 simulation from the representative concentration pathway 8.5 (RCP8.5) scenario, the radiation limitation becomes stronger for both spring and autumn (Fig. 5). At high latitudes (>50° N) where the autumn radiation limitation is already strong, the limitation further increases by $10.0 \pm 2.4\%$ by the 2090s compared with the 2000s. Changes at middle and low latitudes are not significant, most likely due to a relatively stable EOS date, as many ecosystems are limited by water rather than temperature. This suggests that northern ecosystems will increasingly become carbon sources in autumn because of increased light limitation. However, the overall effect on the carbon cycle may be complicated by the permafrost thawing²⁴ and uncertainties in the temperature sensitivity of respiration²⁵.

The radiation limitation presented in this study considers only the seasonal variation of vegetation and Earth–Sun geometry-induced



Fig. 3 | Relationship between temperature anomaly and NEE for spring and autumn at 28 eddy covariance flux tower sites. a,b, Spring (**a**) and autumn (**b**) are defined as the 60-day intervals centred at the multiyear average SOS and EOS derived from GPP. The colours and symbols of the scattered points represent ecosystem types and individual sites. The colours of the regression lines for each site are used to indicate the radiation limitation on photosynthesis. The inset in **a** shows the locations of the 28 flux tower sites. The inset in **b** shows the statistics of the radiation limitation (%) for negative (–) and positive (+) temperature sensitivity on autumn NEE. The horizontal solid lines mark the median values, the boxes indicate the upper and lower quantiles, and the whiskers indicate the range of all samples. The numbers in parentheses indicate the number of sites in each group. T, temperature.



Fig. 4 | Latitudinal comparison of radiation limitations derived from CSIF and CMIP5 models. a,**b**, Radiation limitations by latitude in spring (**a**) and autumn (**b**). The radiation limitation $(1-\gamma)$ calculated from CSIF is used as the reference (black). The median values of each latitude bin (0.5° for CSIF and the model resolution for the CMIP5 models) were used to show the average latitudinal pattern for each model. For clarity, the CMIP5 models were grouped by the land models they used (Supplementary Table 4), with the lines and shades showing the group means and within-group variations (mean ±1s.d.).

changes; it does not consider changes in cloud coverage and the resultant changes in a warming climate, since these can be stochastic and difficult to measure²⁶. This analysis also provides a possible explanation for the photoperiod limitation on plant phenology. When the radiation limitation is strong (usually corresponding to a short day length), keeping leaves would be unwise since it would increase respiratory carbon loss while the photosynthetic gain is limited. Our analyses also indicate an upper physical bound for ecosystems to sequester carbon due to the limited light in early or late growing seasons. Global warming induces faster temperature changes than the vegetation responses²⁷, and diminishing temperature dependence of spring leaf unfolding²⁸ and carbon uptake in northern ecosystems²⁹ has been observed. These lines of evidence suggest that the relative importance of radiation limitation may increase in the spring as the climate warms, resulting in a smaller temperature sensitivity to spring carbon uptake. Previous studies report positive effects of the growing season temperature on ecosystem carbon uptake in high-latitude ecosystems³⁰; however, a negative temperature effect is found toward the EOS due to the strong radiation limitation in these regions. If the autumn dormancy date also keeps delaying with warming, radiation limitation will become increasingly important moving forward, causing a larger region to release carbon with autumn warming. The faster rate of warming in autumn may further exaggerate this carbon loss and ultimately reverse the warming effect on ecosystem carbon uptake. Improving the vegetation phenology in Earth system models may reduce the



Fig. 5 | **Future radiation limitation simulated by CMIP5 models under the RCP8.5 scenario. a**,**b**, Radiation limitation in the spring (**a**) and autumn (**b**). The solid lines represent the multimodel ensemble means, and the shading represents the mean \pm s.d. The limitation is calculated for each year, and the median values during each period (for example, 2020-2039) were used to represent the average radiation limitation.

model spread in predicting the radiation limitation. Continued satellite and in situ observations will help quantify the changes of radiation limitation and better predict the temperature effect on the carbon cycle and the capacity of northern ecosystems to act as carbon sinks.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/ s41558-020-0806-0.

Received: 4 April 2019; Accepted: 5 May 2020; Published online: 06 July 2020

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Methods

Datasets. We used the 16-day, 0.05-degree NDVI and EVI data from MOD13C1 (Collection 6) in 2001–2017 to retrieve the greenness-based phenology. To exclude the possible snow effect, additional night-time land surface temperatures from MYD11C2 (Collection 6) were used to calculate a thermal growing season (see below). Since the data quality and presence of snow are critical for the successful retrieval of phenology³¹, a rigorous data quality check and preprocessing are necessary before the phenology retrieval.

We used four weighted algorithms to extract phenology from both VIs and CSIF. We assigned each observation a weight value that represents the confidence in data quality, so that the fitted smoothed curves are more dependent on high-quality observations. These weight coefficients were adopted from the R package 'phenofit' v.3.5.2 (https://github.com/kongdd/phenofit) with slight modifications. Using the 'Pixel Reliability' layer associated with the NDVI and EVI dataset, we first set the 'cloudy', 'Snow/Ice' and 'Estimated' pixels during the thermal growing season to 'NA', and the corresponding weight to the minimum (0.2) (Extended Data Fig. 3 and Supplementary Table 1). The thermal growing season was determined by the night-time (1:30 local time) land surface temperature when greater than 0 °C (ref. 32). For 2001 and 2002, when land surface temperature observations were missing/incomplete, the multiyear seasonal averages were used. The non-growing-season NDVI or EVI (VInon-gs) values represent the baseline vegetation condition and affect the retrievals of the phenology. To get these time-invariant values for each pixel, we searched all 'Good-quality' observations during the thermal growing season for the entire study period (2001-2017) and chose the minimum value as VI_{non-ss} after outlier rejection (3 σ limits). All observations smaller than this VI_{non-gs} would be replaced by VI_{non-gs}. The weights for these non-growing-season observations were set to 0.5. This 0.5 weight value is chosen as a balance between confidence in data quality and effectiveness in constraining the curve fitting at these turning points. The 'NA' values created in the initial data quality check were then linearly interpolated. Four weighted phenological retrieval algorithms were then applied to these time series.

The CSIF dataset was used to retrieve the carbon-flux-based phenology. This dataset is generated by a machine learning method using MCD43C1 C6 reflectance as inputs¹⁰. The machine learning algorithms were trained on the daily OCO-2 SIF observations with colocation nadir BRDF-adjusted reflectance. This dataset can capture the seasonal and spatial variability of the raw OCO-2 SIF at the far-red band (767 nm), which is demonstrated to strongly relate to spatio-temporal variation of GPP (refs. ^{11,33,34}). In this study, we used the clear-sky daily CSIF (CSIF_{clear-daily}) with a four-day temporal and 0.05° spatial resolution. The clear-sky product is selected since it has a stronger correlation with the satellite retrievals, and also strong correlations with GPP estimates from eddy covariance flux towers^{16,35}. The different slopes between CSIF and GPP across ecosystem types do not alter our retrievals of SOS and EOS, as all algorithms are based on normalized values between 0 and 1.

For CSIF, since the initial quality check and gap filling were applied to the reflectance before the dataset production, we only checked the CSIF values using two criteria: (1) the CSIF values smaller than zero were replaced with zero, and the corresponding weights were set to 0.5; and (2) using 17 years of CSIF, we calculated the mean seasonal average and standard deviation. For each year, observations outside the 3σ limits were linearly interpolated, and the corresponding weights were set to 0.2.

To test the robustness of the radiation limitation derived from CSIF, we used an independent SIF dataset from GOME-2 (ref. ³⁶). We did not use SIF from the TROPOspheric Monitoring Instrument (TROPOMI) because it did not provide a full annual cycle until recently³⁷. The v27 monthly SIF suffers from large uncertainties and a decreasing trend caused by sensor degradation³⁸. We therefore calculated the mean seasonal cycle of daily average SIF in 2007–2017 and derive SOS, EOS and their corresponding radiation limitations from this mean seasonal cycle.

We used the FLUXNET2015 Tier 1 to analyse the radiation limitation and its effects on NEE temperature sensitivity. The GPP estimates from the night-time partitioning method³⁹ were used for the analysis. A rigorous site selection was conducted to eliminate the artefacts related to data quality and human management. We first select the site-years that had valid observations during the growing season (gap-filled NEE observations less than 50% for each month between April and October). Only sites with more than five years of observations were considered (60 sites). We then dropped all cropland sites and intensively managed grassland sites since their phenology and carbon balance are disturbed by human intervention (45 sites remaining). Additionally, the carbon fluxes for wetland sites are influenced by upstream organic matter and nutrient input⁴⁰, as well as fluctuating water tables⁴¹; these sites were also removed (43 sites remaining). Since for some water-limited shrubland and forest sites, temperature is not the major limitation for the growing season length and carbon uptake, these sites were also excluded (28 sites remaining, Supplementary Table 2).

We used 26 CMIP5 models to examine the radiation limitation and its relationship with the temperature sensitivity of net ecosystem production (Supplementary Table 4). Monthly GPP, autotrophic and heterotrophic respiration and surface air temperature estimations from historical runs (1985–2004) were used. We also used monthly GPP estimates under RCP8.5 to derive the radiation limitation in the future.

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Phenology retrieval. Weighted spline threshold method (wSpline-Thr). For each year, the VI or CSIF observations with weights were first fitted to a cubic smoothing spline model⁴² with a degree of freedom (trace of the smoother matrix) of 7 (for VI) or 9 (for CSIF or eddy covariance GPP). The fitted spline model was used to predict VI or CSIF for each day of the year. The mean seasonal average was calculated, and the minimum value plus 30% of the amplitude was used as the pixel-specific threshold. This threshold was then used for both spring and fall to extract the SOS and EOS. A lower or higher threshold value only changes the absolute value of the SOS and EOS date and has little effect on the interannual variability and trend¹⁰.

Weighted harmonic analysis of time series maximum rate method (wHANTS-MR). The wHANTS-MR method first fits the normalized yearly observations with weights into a series of harmonic functions (three for VI and four for CSIF) with different frequencies (yearly, every 6 months, every 3 months and possibly every 1.5 months)⁴³. The fitted model then predicts the VI or CSIF for each day of the year. To get the threshold to derive the SOS and EOS, the multiyear mean seasonal average was calculated using the raw data. The change of VI and CSIF at each time step (every 16 days for VI and every 4 days for CSIF) was calculated, and the dates before the maximum change (positive value) and after the minimum change (negative value) were selected⁴⁴. The corresponding VI or CSIF values for these two days were used as thresholds to derive the SOS and EOS, respectively.

Weighted polynomial fit maximum rate method (wPolyfit-MR). The wPolyfit-MR method first fits the yearly observations into a six-order (eight-order for CSIF) polynomial⁴⁴. The fitted model predicts the VI or CSIF for each day of the year. The thresholds used to retrieve the SOS and EOS were calculated similarly as for wHANTS-MR.

Weighted double logistic method (wDoubleLog). The weighted piecewise logistic method fits the yearly VI or SIF observations into a pair of sigmoidal functions:

$$f(t) = a_1 + \frac{a_2}{1 + e^{-\theta_1(t-\beta_1)}} - \frac{a_3}{1 + e^{-\theta_2(t-\beta_2)}}$$
(1)

where a_1 represents the minimum value of the seasonal cycle, and a_2 and a_3 represent the amplitudes of the seasonal cycle in the first and second halves (due to potentially different background values in pre-spring and late autumn). θ_1 and θ_2 are empirical coefficients that determine the speed of vegetation growth and senescence. SOS and EOS are determined as the curvature changing rate reaches its local maximum ($\beta_1 - 1.317/\theta_1$ for SOS, and $\beta_2 + 1.317/\theta_2$ for EOS), after this seven-parameter model is fitted⁴⁵.

During model optimization, we used the weighted root mean square error as the cost function, so the observations with smaller weights have a smaller contribution to the model fitness. For three threshold-based methods (wSpline-Thr, wHANTS-MR and wPolyfit-MR), if multiple growing seasons exist within one year (that is, the smoothed time series crosses down the autumn threshold more than once), only the one with the maximum VI/CSIF was used to retrieve the phenology. It should be noted that although the temporal resolutions range from daily to monthly for the input datasets, they were interpolated to daily resolution using the three smoothing methods (except wDoubleLog, which can directly derive SOS and EOS after model fit) before phenology retrieval.

For the VI and CSIF datasets, the multiple-method averages and trends for SOS and EOS were first calculated within each model using the non-parametric Theil-Sen estimator (Supplementary Figs. 1 and 2), and the medians were used as the multimethod ensemble.

Calculation of radiation limitation. Because of the strong correlation between GPP and SIF in the temporal domain, the GPP–CSIF relationship can be expressed as:

$$GPP = \beta \times CSIF = LUE \times fPAR \times PAR$$
(2)

where β is a pixel-specific empirical coefficient that links CSIF to GPP. Since phenology is analysed for each individual pixel, and the GPP and CSIF have similar seasonal trajectories and only percentage changes are needed for phenology retrievals, CSIF can be used to replace GPP for the analysis below. Here we use the potential clear-sky top-of-canopy PAR (PAR_{clear-sky}) to represent the PAR in equation (2), so that it can be analytically calculated using the cosine of the solar zenith angle and the elevation (see the detailed information in ref. ¹⁶). The cloudiness-induced PAR variations can thus be considered as part of LUE (cloud effect on LUE, which affects not only incident PAR but also the direct/diffused radiation⁴⁶). In this way, the radiation limitation can be regarded as a physical limitation caused by the seasonal change of Sun–Earth geometry and can remain unchanged with interannual variations of cloudiness.

We use the EOS as an example to illustrate the analytical framework. The sensitivity of the GPP-based EOS to the extension of the greenness-based EOS (γ_{EOS}) can be calculated by considering two scenarios (Extended Data Fig. 4), as follows.

At the initial GPP-based EOS (EOS₀):

$$GPP_{threshold} = LUE_0 \times fPAR_0 \times PAR_0$$
(3a)

When LUE \times fPAR is delayed by one day, the GPP-based EOS is delayed by γ_{EOS} days (EOS1):

$$GPP_{threshold} = LUE_1 \times fPAR_1 \times PAR_1$$
(3b)

At this new EOS date (EOS1), LUE \times fPAR increases by $(\gamma_{EOS}-1)\times\frac{d(LUE\times fPAR)}{dt}$

(Δ (fPAR×LUE) in Extended Data Fig. 4b), and PAR decreases by $\gamma_{EOS} \times \frac{dPAR}{dt}$ (Δ PAR in Extended Data Fig. 4b):

$$LUE_{1} \times fPAR_{1} = LUE_{0} \times fPAR_{0} + (\gamma_{EOS} - 1) \times \frac{d(LUE \times fPAR)}{dt}$$
(4a)

$$PAR_{1} = PAR_{0} + \gamma_{EOS} \times \frac{dPAR}{dt}$$
(4b)

The LUE \times fPAR increase will be compensated by the decrease of PAR, so that the GPP_{threshold} will remain unchanged:

$$GPP_{threshold} = \left(LUE_0 \times fPAR_0 + (\gamma_{EOS} - 1) \times \frac{d(LUE \times fPAR)}{dt}\right) \times (PAR_0 + \gamma_{EOS} \times \frac{dPAR}{dt}) = LUE_0 \times fPAR_0 \times PAR_0$$
(5)

We can determine γ_{EOS} by solving this equation (5):

$$\gamma_{\rm EOS} = \frac{ab - a - b \pm \sqrt{4a^2b + (ab - a - b)^2}}{2ab}$$
(6)

where a and b represent the normalized derivatives of LUE \times fPAR and PAR to

time at point EOS₀ $\left(a = \frac{d(LUE \times fPAR)}{dt} / (LUE_0 \times fPAR_0), b = \frac{dPAR}{dt} / PAR_0\right)$ Only the positive root between 0 and 1 will be kept. The variable *b* can be analytically solved for each pixel given the EOS date and latitude. Two strategies were adopted to calculate *a*:

- (1) If we assume that only PAR_{clear-sky} changes to compensate for the change of LUE × fPAR (in other words, if γ_{EOS} describes the relative importance of PAR to all other factors for GPP (that is, LUE × fPAR)), then $1 \gamma_{EOS}$ represents the exclusive PAR limitation on GPP. LUE × fPAR can be calculated from GPP (for EC sites or for CMIP5 models) or CSIF (LUE × fPAR = $\frac{\beta \times CSIF}{PAR_{dear-sky}}$, and the seasonal cycle of LUE × fPAR is then used to calculate the normalized derivative at EOS (*a* in equation (6)). We denote this calculation as $\gamma_{EOS_{CSIF}}$ or $\gamma_{FOS_{CMN}}$.
- (2) If we assume that environmental limitations (for example, temperature) change as the EOS shifts (that is, LUE₁ equals LUE₀), equation (5) can be rewritten as:

$$\left(fPAR_{0} + (\gamma_{EOS} - 1) \times \frac{dfPAR}{dt}\right) \times \left(PAR_{0} + \gamma_{EOS} \times \frac{dPAR}{dt}\right) = fPAR_{0} \times PAR_{0}$$
(7)

Under this situation, γ_{EOS} describes the relative importance of PAR to fPAR only, and $1-\gamma_{EOS}$ represents the PAR limitation together with other limitations on LUE such as temperature. The value of fPAR in this situation can be derived from the NDVI dataset (fPAR=1.24 \times NDVI-0.168) (ref. 47). The factor 0.168 was used to adjust the non-vegetated background value. The seasonal cycle was calculated as a weighted average of quality-checked NDVIs. We denote this calculation as $\gamma_{EOS_{STVI}}$.

For spring, equation (5) has a different form:

$$\left(LUE_0 \times fPAR_0 + (1 - \gamma_{SOS}) \times \frac{d(LUE \times fPAR)}{dt} \right) \times \left(PAR_0 - \gamma_{SOS} \times \frac{dPAR}{dt} \right)$$

$$= LUE_0 \times fPAR_0 \times PAR_0$$
(8)

With a solution of:

$$\gamma_{\rm SOS} = \frac{ab+a+b\pm\sqrt{(ab+a+b)^2-4a^2b}}{2ab} \tag{9}$$

The radiation limitation $(1 - \gamma)$ can be calculated from GPP (from EC or CMIP5) or SIF (CSIF) observations for each year. SOS and EOS were first derived using the wSpline-Thr method; the LUE×fPAR values were then calculated from the smoothed GPP or CSIF by normalizing it with top-of-canopy clear-sky radiation. The normalized derivatives for LUE×fPAR and PAR (*a* and *b*, respectively, in equation (6)) were then obtained to calculate γ_{SOS} and γ_{EOS} . The median value for the available years was used to represent the average radiation limitation for each site or grid cell. Since parameters *a* and *b* in equation (6) are

also affected by the threshold used in the wSpline-Thr method, we also tested two different thresholds (25% and 35% of the seasonal magnitude) and compared their spatial patterns. For the γ derived from the CSIF dataset, we also calculated the trend of γ in 2001–2017 using the non-parametric Theil–Sen estimator.

Temperature sensitivity of net ecosystem uptake. To get the temperature sensitivity from the EC measurements or CMIP5 models, SOS and EOS were first derived for each year using the wSpline-Thr method. Spring and autumn were considered as the 60-day intervals around the multiyear average SOS and EOS, respectively. The average temperature and NEE were then calculated for each year, and the NEE temperature sensitivity was calculated as the regression slope between spring/autumn NEE and the spring/autumn temperature for each site.

Changes of radiation limitation to the extension of the growing season. Within the normal range of the percentage change of fPAR (*a* in equations (6) and (9)), γ_{SOS} monotonically decreases as the percentage change of PAR (*b* in equations (6) and (9)) increases in the spring, and γ_{EOS} monotonically increases with an increase in *b* in the autumn. Assuming that the slopes of the fPAR increase (in the spring) and decrease (in the autumn) do not change (that is, *a* does not change), changes in *b* due to the growing season extension directly lead to the changes in γ . We analysed the variation of *b* as a function of latitude and day of the year. By comparing this variation with the latitudinal pattern of multiyear average SOS and EOS, we can evaluate whether the extension of the growing season would increase or decrease *b* and γ in the spring and autumn (Extended Data Fig. 8). Our results show that with the extension of the growing season, both spring and autumn are expected to have smaller γ and therefore greater radiation limitation.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The MODIS VI and land surface temperature data are from https://lpdaac.usgs. gov/node/841 and https://lpdaac.usgs.gov/node/834, the CSIF data are from https://doi.org/10.17605/OSFIO/8XQY6, the FLUXNET2015 dataset is from http:// fluxnet.fluxdata.org/data/fluxnet2015-dataset/ and the CMIP5 model simulations are from https://esgf-node.llnl.gov/search/cmip5/. Raw data for Figs. 1–5 are available via FigShare at https://doi.org/10.6084/m9.figshare.11986764.

Code availability

The code used for the phenology retrieval and data analysis are available from Y.Z. upon request.

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Acknowledgements

This work used eddy covariance data acquired and shared by the FLUXNET community, including these networks: AmeriFlux, AfriFlux, AsiaFlux, CarboAfrica, CarboEuropeIP, CarboItaly, CarboMont, ChinaFlux, Fluxnet-Canada, GreenGrass, ICOS, KoFlux, LBA, NECC, OzFlux-TERN, TCOS-Siberia and USCCC. The ERA-Interim reanalysis data are provided by ECMWF and processed by LSCE. The FLUXNET eddy covariance data processing and harmonization were carried out by the European Fluxes Database Cluster, AmeriFlux Management Project and Fluxdata project of FLUXNET, with the support

of CDIAC and ICOS Ecosystem Thematic Center, and the OzFlux, ChinaFlux and AsiaFlux offices. Y.Z. acknowledges funding from NASA ROSES Advanced Information System Technology (grant no. 80NSSC17K0285). P.G. acknowledges support from NASA ROSES Terrestrial Hydrology (grant no. 80NSSC18K0998), NOAA MAPP (grant no. NA17OAR4310127) and European Research Council (grant no. CU18-3746). A.P.W. acknowledges support from the NASA Modeling, Analysis, and Prediction (MAP) programme (grant no. NASA 80NSSC17K0265).

Author contributions

Y.Z. and P.G. conceived and designed the study. Y.Z. performed the data analysis. Y.Z., S.Z., R.C., A.P.W. and P.G. contributed to the interpretation of the results. Y.Z. drafted the manuscript. All authors participated in discussions and the editing of the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

Extended data is available for this paper at https://doi.org/10.1038/s41558-020-0806-0. **Supplementary information** is available for this paper at https://doi.org/10.1038/

s41558-020-0806-0.

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Peer review information *Nature Climate Change* thanks Su-Jong Jeong and the other, anonymous, reviewer(s) for their contribution to the peer review of this work.

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Extended Data Fig. 1 | Comparison between CSIF OCO-2 SIF and GPP at multiple scales. a Comparison between OCO-2 SIF (SIF_{oco-2}), CSIF, NDVI and EVI for the northern ecosystems (>30°N). The error bands associated with SIF_{oco-2} and CSIF represent the standard deviation of all observations in northern ecosystems, with the solid lines for the mean. For readability, error bands for NDVI and EVI are not shown. **b-g** Comparison between the spring growth onset and autumn dormancy onset derived from CSIF and flux tower estimated GPP at 40 sites from the FLUXNET2015 tier 1 dataset (Supplementary Table 3). **b** Locations of the 40 sites. **c** Comparison between eddy-covariance (EC) estimated GPP and CSIF at 4-day temporal resolution. **d**, **e** Comparison between SOS and EOS derived from EC estimated GPP and CSIF for all site-years. **f**, **g** Comparison between the interannual anomaly of SOS and EOS (Δ SOS and Δ EOS) for each site. The anomalies were calculated as the phenological dates for each year minus the multi-year average. Only sites with at least 5 years of observations were used for this interannual comparison.

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Extended Data Fig. 2 | Average growth onset and dormancy onset for 2001-2017 for four vegetation indicators. a, b NDVI, c, d EVI and e, f CSIF, g, h GOME-2 SIF. The median value from four methods (wSpline-Thr, wHANTS-MR, wPolyfit-MR, wDLogistic) were shown. The growth onset and dormancy onset for GOME-2 SIF were derived from a mean seasonal cycle between 2007-2017, while others were derived for each year and averaged over the entire period.

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Extended Data Fig. 3 | MODIS VI processing schemes for phenology retrieval. The nighttime LST (1:30 am local time) from Aqua satellite were used as it is close to the minimum LST.



Extended Data Fig. 4 | A schematic diagram showing the extension of fPAR based growing season and its impact on GPP based growing season. Left panels show how γ can be calculated. **b** shows a zoom in of autumn dormancy from schematic seasonal cycles **a**. Solid blue line in **b** represents the original fPAR×LUE and dashed-lines shows that with one day delay (corresponding to a one-day delay of greenness-based EOS). As a result, GPP based EOS delayed by γ day, from EOS₀ to EOS₁. Open circles and dots in **b** indicate the fPAR×LUE and PAR values for EOS₀ and EOS₁, respectively. At this new EOS date, fPAR×LUE increases by Δ (fPAR×LUE) and PAR decreases by Δ PAR. Note that Δ (fPAR×LUE) does not equal to Δ PAR, but rather $\left[1 + \frac{\Delta(fPAR\times LUE)}{fPAR\times LUE}\right]\left[1 - \frac{APAR}{PAR}\right] = 1$ (see Methods). The right panels show two examples of how latitude and plant species (evergreen or deciduous) may affect γ values. Both PAR and fPAR×LUE in **c** and **d** were normalized by the PAR and fPAR×LUE values at EOS₀, respectively. With increases in latitude, γ decreases, suggesting an increase in radiation limitation. Evergreen forests also exhibit relatively smaller γ values compared to deciduous species because of the relatively smaller percentage decrease of fPAR×LUE.



Extended Data Fig. 5 | Comparison between radiation limitation derived from CSIF and that derived from GOME-2 SIF. Left column is for spring and right column is for autumn.



Extended Data Fig. 6 | Comparison between the radiation limitation using different threshold values to retrieve SOS and EOS. Three thresholds for wSplineThr method to retrieve SOS and EOS were compared here. **a,b** threshold is minimum +30% of the seasonal magnitude, **c,d** threshold is minimum +25%, of the seasonal magnitude, **e,f** threshold is minimum +35% of the seasonal magnitude. The difference in radiation limitation between the 35% and 25% thresholds is 0.9% (95% confidence interval: -2.1% to 14.0%).



Extended Data Fig. 7 | Trend in the change of radiation limitation (1-γ) during 2001-2017. Pie charts shows the areal percentages with decreasing trend ('-') or increasing trend ('+').



Extended Data Fig. 8 | Change of normalized derivative of PAR (parameter *b* **in Equations. 6 or 9) along latitude and season.** Thick solid lines represent the median value of multi-year average SOS and EOS along latitude. Thin dashed and dotted lines represent the timings when *b* reaches maximum or minimum for each latitude bins, respectively. In the spring, advancing of the SOS would lead to increase of *b* and thus a greater radiation limitation. In the autumn, delaying of the EOS would lead to decrease of *b* until the minimum, also leading to a greater radiation limitation.



Extended Data Fig. 9 | Correlation between temperature sensitivity of autumn NEE (γ_T^{NEE} **) and radiation limitation.** Positive γ_T^{NEE} values indicate that ecosystem will release carbon (postive NEE) when temperature increases. Shaded area indicate 95% confidence interval of the regression.



Extended Data Fig. 10 | Radiation limitation and temperature responses of autumn NEE for CMIP5 models. Net ecosystem exchange (NEE) is calculated as the summation of autotropic and heterotopic respiration minus gross primary production, with a negative value indicates a carbon sink. Similar with inset in Fig. 3b, autumn NEE sensitivity is categorized into increase (blue) or decrease (red) carbon uptake with autumn warming. Only the gridcells that are limited by temperature is used for analysis (GPP based EOS delays when autumn temperature increases). Autumn is defined as 60 days interval around the GPP determined multi-year average EOS date. GPP, ecosystem respiration (Ra+Rh) and air temperature were interpolated from monthly to daily values to get the autumn average. Upper and lower boundary of the boxes represent the 25 and 75 percentiles, with the white lines in the middle the median values. The horizontal dashed green dashed line indicates the threshold to separate the negative and positive temperature sensitivity to ecosystem autumn NEE based on flux tower analysis. The grey shaded area represents the standard deviation of the threshold estimated by bootstrapping (n=2000). *** represent significance level at 0.001.

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Last updated by author(s): Mar 13, 2020

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Data collection	No software was used to collect data.					
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Study description	This study presents satellite and flux tower derived radiation limitions on vegetation photosynthesis during spring and autumn, and investigates how these limitations affect the ecosystem carbon uptake in response to warming.					
Research sample	We used a newly developed contiguous SIF (CSIF) dataset, satellite derived NDVI and EVI datasets, and satellite retrieved SIF from GOME-2. We used daily carbon fluxes estiamtes and climate measurements from the FLUXNET datasets. We also used monthly GPP, ER and air temperature from 26 CMIP5 models for historical run and 21st century prediction under RCP8.5 scenario.					
Sampling strategy	We used satellite data for vegetated land in northern latitude. We used all flux tower sites that meet the criteria, representing major land cover types in the study region.					
Data collection	All dataset were downloaded using the URLs in the data availability statement in the main text.					
Timing and spatial scale	The contiguous SIF has a 4-day temporal resolution and 0.05 degree spatial resolution. Satellite derived NDVI, EVI dataset have a 16- day temporal resolution and 0.05 degree spatial resolution. The CSIF, NDVI and EVI were from 2001-2017. The GOME-2 SIF has a monthly temperol resolution and 0.5 degree spatial resolution during 2007-2017. Eddy covariance flux data measures gas exchanges and climate variables at a footprint size of hundreds meters to several kilometers. Observations during 1992-2014 were used based on availability by site. Details can be seen in Supplementary Table 2 and 3.					
Data exclusions	We did not exclude any data, but the flux tower sites were selected based on certain criteria. Details can be found in Methods section.					
Reproducibility	Our analyses were based on public satellite products and well-defined methods, the results could be reliably reproduced.					
Randomization	Randomization is not apply to this study as we performed wall-to-wall mapping globally with satellite images.					
Blinding	Our study only used existing data, therefore blinding is not relevant to our study.					
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