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Urban–rural gradients reveal joint control of elevated CO₂ and temperature on extended photosynthetic seasons

Songhan Wang¹,²,³, Weimin Ju¹,², Josep Peñuelas⁴,⁵, Alessandro Cescatti⁶, Yuyu Zhou⁷, Yongshuo Fu⁸, Alfredo Huete⁹, Min Liu¹⁰,¹¹, Yongguang Zhang¹,²,³*

¹International Institute for Earth System Sciences, Nanjing University, Nanjing, China.
²Jiangsu Center for Collaborative Innovation in Geographical Information Resource Development and Application, Nanjing, China.
³Collaborative Innovation Center of Novel Software Technology and Industrialization, Nanjing, 210023, China.
⁴CSIC, Global ecology Unit CREAF-CSIC-UAB, Bellaterra 08193, Catalonia, Spain.
⁵CREAF, Bellaterra 08193, Catalonia, Spain.
⁶European Commission, Joint Research Centre, Directorate for Sustainable Resources, Ispra, Italy.
⁷Department of Geological and Atmospheric Sciences, Iowa State University, Ames, IA 50011, USA.
⁸College of water sciences, Beijing Normal University, Beijing, China.
⁹School of Life Sciences, University of Technology Sydney, NSW 2007, Australia.
¹⁰Institute of Eco-Chongming, Shanghai 200062, China.
¹¹Shanghai Key Laboratory for Urban Ecological Processes and Eco-Restoration, School of Ecological and Environmental Sciences, East China Normal University, Shanghai 200241, China.

*Corresponding author:
Yongguang Zhang
International Institute for Earth System Sciences
Nanjing University
163 Xianlin Avenue, Qixia District, Nanjing, Jiangsu Province, China
Email: yongguang_zhang@nju.edu.cn
Tel. +86-(0)25-89681569
Abstract

Photosynthetic phenology has large effects on the land-atmosphere carbon exchange. Due to limited experimental assessments, a comprehensive understanding of the variations of photosynthetic phenology under future climate and its associated controlling factors is still missing, despite its high sensitivities to climate. Here we develop an approach that uses cities as natural laboratories, since plants in urban areas are often exposed to higher temperature and carbon dioxide (CO$_2$) concentration, which reflect expected future environmental conditions. Using more than 880 urban–rural gradients across the Northern Hemisphere ($\geq 30^\circ$), combined with concurrent satellite retrievals of sun-induced chlorophyll fluorescence (SIF) and atmospheric CO$_2$, we investigated the combined impacts of elevated CO$_2$ and temperature on photosynthetic phenology at large scale. Results show that in urban conditions of elevated CO$_2$ and temperature, vegetation photosynthetic activity began earlier ($-5.6 \pm 0.7$ days), peaked earlier ($-4.9 \pm 0.9$ days) and ended later ($4.6 \pm 0.8$ days) than in neighboring rural areas, with a striking two- to four-fold higher climate sensitivity than greenness phenology. The earlier start and peak of season were sensitive to both the enhancements of CO$_2$ and temperature, whereas the delayed end of season was mainly attributed to CO$_2$ enrichments. We used these sensitivities to project phenology shifts under four “Representative Concentration Pathway” (RCP) climate scenarios, predicting that vegetation will have prolonged photosynthetic seasons in the coming two decades. This observation-driven study indicates that realistic urban environments, together with SIF observations, provide a
promising way for vegetation physiological studies under future climate change.
Terrestrial ecosystems absorb approximately one quarter of the anthropogenic carbon dioxide (CO$_2$) released into the atmosphere, which effectively mitigates climate warming$^1$. The timing and duration of vegetation photosynthetic activity (i.e., photosynthetic phenology), play an important role in the carbon cycle of land ecosystems$^{2,3}$ and are strongly affected by climate change$^4$-$^7$. Understanding the response of photosynthetic phenology to increasing atmospheric CO$_2$ concentrations and global warming is, therefore, essential to better understand the future dynamics of the terrestrial carbon cycle$^8$-$^9$ and formulate land-based strategies to mitigate climate change$^{10}$. Current experimental assessments of the effects of climate warming and CO$_2$ fertilisation on plant phenology have generally been restricted to manipulated experiments$^{11,12}$ with very limited spatial extent and species coverage, which may ultimately led to ambiguous and controversial findings$^{13}$. In particular, the role of CO$_2$ fertilisation on tree phenology remains largely unknown in real natural settings. Moreover, many field experiments have been recently terminated because of their high cost$^{14}$, thus limiting consistent long-term observations and reinforcing the need for effective, low-cost alternative monitoring approaches.

In this analysis, we make use of contrasting conditions in urban–rural environments, serving as “natural laboratories” to conduct a novel, and first time investigation on the combined effects of future global warming and CO$_2$ fertilisation on vegetation phenology at a very large scale$^{14}$. Because of the urban heat island effect$^{15}$ and the larger CO$_2$ emissions from fossil-fuel combustion$^{16}$, vegetation in urban areas is typically exposed to
higher temperatures and CO₂ concentrations than in rural areas and are therefore experiencing growing conditions projected for the future. Assuming that phenology responds similarly to altered temperature and atmospheric CO₂ in urban and rural areas, the urban–rural gradients can be considered as “natural experiments” with similar photoperiod and weather, and at lower costs than manipulation experiments. Using the space-for-time substitution concept, we therefore used the physiological dynamics of vegetation across urban–rural gradients to investigate the effects of future global warming and CO₂ fertilisation on photosynthetic phenology. Data were collected from 880 urban clusters and their adjacent rural areas at mid- to high-latitudes in the Northern Hemisphere (NH, ≥30°) (Supplementary Fig. 1). Photosynthetic phenology was extracted from the Orbiting Carbon Observatory-2 (OCO-2) sun-induced chlorophyll fluorescence (SIF, a proxy for photosynthesis) data, which are highly correlated with photosynthetic rates and can monitor actual photosynthetic dynamics. We used the traditional, satellite greenness phenology for comparison, which was extracted from Moderate Resolution Imaging Spectroradiometer (MODIS) Enhanced Vegetation Index (EVI). The urban–rural surface CO₂ gradients were obtained through a conversion approach with OCO-2 column-averaged CO₂ mixing ratios (XCO₂) data (see Methods). The primary objective of our analysis was to determine the differences in photosynthetic phenology across urban–rural gradients and explore the combined effect of atmospheric CO₂ enrichment and warming on plant photosynthetic phenology at a very large scale. Phenological differences and environmental gradients were then used to quantify the
sensitivities of the processes and ultimately to project shifts in phenophases under contrasting climate scenarios.

**Results**

We found that vegetation showed a larger than expected anticipation and prolongation of the photosynthetic season within urban environments. On average, the SIF-based photosynthetic activity began 5.6 days earlier, peaked 4.9 days earlier, ended 4.6 days later and lasted 10.2 days longer in urban than in rural areas (Fig. 1). These variations were two- to four-times larger than those in greenness phenology derived from MODIS EVI, due to the significantly higher urban–rural $\Delta$SIF than $\Delta$EVI during spring and autumn (Supplementary Fig. 2). The timing of each phenological indicator we examined (SOS, start of growing season; POS, peak of growing season; EOS, end of growing season; GSL, length of growing season) was generally highly correlated between urban areas and neighbouring rural counterparts, but with significant systematic deviations, as indicated by the slopes of the regression lines (Supplementary Fig. 3). The SOS and POS occurred earlier in urban areas as suggested by the slopes of larger than one (i.e., 1.01–1.03 and 1.00–1.02; $p < 0.001$) for the regression lines, whereas the EOS occurred later in urban areas as indicated by the slopes of lower than one (i.e., 0.98–0.99; $p < 0.001$). On average within cities, SOS and POS were therefore advanced, while EOS was delayed and GSL was extended for the phenology of SIF. Similar patterns were found for the phenology of EVI, but the magnitudes of these changes were substantially smaller than that of SIF (Supplementary Fig. 4) (about four-fold for $\Delta$SOS and $\Delta$POS,
two-fold for \( \Delta \text{EOS} \) and three-fold for \( \Delta \text{GSL} \); Fig. 1). The larger differences of photosynthetic phenology in urban–rural gradients than the differences of greenness phenology were not affected by the mismatching in the spatial resolutions of SIF and EVI data, as also tested after resampling to the same resolution (Supplementary Fig. 5). These results suggest a remarkable shift in the response of photosynthetic phenology to urban environmental conditions in the mid- to high-latitudes of the NH. These variations cannot be completely explained by the variations in greenness phenology based on VIs or leaf area index (LAI) and probably involve physiological responses to environmental drivers.

Vegetation in urban areas generally had earlier photosynthetic SOS and POS, later EOS and longer GSL in the NH across various latitudes and climatic backgrounds (Fig. 2). On average, more than 70% of the urban clusters had longer photosynthetic seasons than rural buffers. \( \Delta \text{SOS} \) and \( \Delta \text{POS} \) were lower than zero days across the whole NH, while most of the \( \Delta \text{EOS} \) were greater than zero days, suggesting that the trends of earlier start/peak and delayed end of photosynthesis in urban environments are common across northern latitudes. Nevertheless, some spatial patterns of phenological shifts along urban–rural gradients were also evident; \( \Delta \text{SOS} \) tended to decrease slightly as latitude increased, \( \Delta \text{EOS} \) and \( \Delta \text{GSL} \) had the highest values at mid-latitudes, whereas \( \Delta \text{POS} \) had no clear trend (second column in Fig. 2). The spatial patterns of SIF \( \Delta \text{SOS} \) were not fully consistent with previous studies conducted with EVI, which showed an increasing trend of EVI \( \Delta \text{SOS} \) with the latitude\(^{21} \) due to the larger urban heat island effects in high-latitudes\(^{15,22} \). This divergence possibly suggests that the spatial distributions of SIF
Urban–rural phenological gradients cannot be explained by temperature alone. Importantly, urban–rural phenological differences were more significant in warm and dry regions (i.e. areas with high mean annual air temperature and low annual precipitation) than in other regions (third column in Fig. 2). Thus, the phenological differences in arid climate zones were significantly higher than that in temperate and boreal areas (Supplementary Fig. 6). These results suggest a general phenomenon that urban environmental conditions extend the photosynthetic seasons and that the impacts in warm and dry regions are greater than those in other climate regions.

Urban–rural phenological difference is likely driven by several interacting factors including the enhancements of temperature and CO$_2$, the geolocation of a city, the urban size and climatic background. Partial correlation analysis showed that SIF $\Delta$SOS and $\Delta$POS were mainly controlled by the daytime urban heat island ($\Delta$LST$_{day}$) effects and urban–rural CO$_2$ gradients ($\Delta$CO$_2$), of which $\Delta$LST$_{day}$ was the most significant (Fig. 3). SIF $\Delta$EOS was mainly attributed to the enhanced CO$_2$ only, resulting in similarly significant effects of temperature and CO$_2$ on $\Delta$GSL (Fig. 3). In order to attribute the effects of environmental drivers on photosynthetic phenology, we further analysed the associations between elevated daytime temperature or atmospheric CO$_2$ and urban–rural phenological differences (Fig. 4). The onset and peak time of photosynthesis were both advanced significantly as atmospheric CO$_2$ concentration increased ($p = 0.013$ and $0.021$, respectively) and as temperature increased ($p = 0.019$ and $0.006$, respectively). The end of photosynthetic activity was significantly delayed as CO$_2$ concentrations increased ($p =$
0.028), whereas its association with temperature was not significant ($p = 0.259$). Our analyses suggest that not only daytime temperature but also atmospheric CO$_2$ have large impacts on photosynthetic phenology of urban plants and, therefore, may potentially inform on the future phenological shifts of natural vegetation under scenarios of warming and atmospheric CO$_2$ enrichment.

Finally, using observations along the urban–rural gradients as natural laboratories, we projected the shifts in photosynthetic phenology for the next two decades using the space-for-time substitution. Based on forward stepwise regression models (see Methods), the sensitivities of $\Delta$SOS, $\Delta$POS and $\Delta$GSL to daytime temperature were $-1.55 \pm 0.60$, $-2.11 \pm 0.78$ and $3.31 \pm 1.10$ days·°C$^{-1}$, respectively (Fig. 5a). The sensitivities of $\Delta$SOS, $\Delta$POS, $\Delta$EOS and $\Delta$GSL to surface CO$_2$ concentration were $-0.15 \pm 0.07$, $-0.18 \pm 0.09$, $0.17 \pm 0.07$ and $0.32 \pm 0.11$ days·ppm$^{-1}$, respectively (Fig. 5b). Given the observed sensitivities and four different “Representative Concentration Pathway” (RCP) scenarios of surface temperature and CO$_2$ concentration$^{10}$ (i.e., RCP 2.6, 4.5, 6.0 and 8.5, Supplementary Fig. 7), we projected the possible shifts of photosynthetic SOS, POS, EOS and GSL from 2015 to 2035 (Fig. 5c-f). Results show that the phenophase shifts were lowest in the RCP 2.6 scenario and highest in the RCP 8.5 scenario. Assuming constant sensitivities for the next two decades, under the range of climate pathways foreseen by RCP scenarios during 2015–2035, the photosynthetic SOS and POS would advance at a rate of 2.8–5.7 and 3.3–6.9 days·decade$^{-1}$, respectively; and the EOS would delay at a rate of 3.1–5.7 days·decade$^{-1}$, prolonging the growing season by a rate of
5.9–11.4 days·decade\(^{-1}\) (Fig. 5g). It should be noted that the responses of vegetation
phenology to temperature are not stationary\(^{23}\) and are likely to decline in the near
decades\(^{9,24}\). Besides, the sensitivity of vegetation phenology to CO\(_2\) may not be static
either in the coming decades, since the projected future concentrations of CO\(_2\) could
exceed the range currently experienced by the urban vegetation (Fig. 4 & Supplementary
Fig. 7b). Therefore, our analysis of the projected photosynthetic phenology based on the
static sensitivity may overestimate the future shifts of vegetation phenophases. This
caveat, however, can be solved in the future by the same procedure introduced in this
study and continued satellite SIF observations.

Discussion

We found systematic differences between urban–rural gradients of photosynthetic
and greenness phenology (Fig. 1). The urbanization effects on vegetation photosynthetic
phenology were more than twofold higher than those on greenness. This phenomenon
could be explained by the significant differences between season cycle of EVI and SIF,
namely EVI shows an earlier spring increase and a later autumn falling than SIF
(Supplementary Fig. 2a). This difference has also been demonstrated by a recent study\(^{25}\).
The timing of carbon assimilation in spring lags behind the leaf burst, which varies with
foliar structure and longevity\(^{26}\). The photosynthetic activity shuts down before the
reduction of leaf chlorophyll and leaf abscission because of the limitation of light
availability\(^{27,29}\). Another possible reason is that urban phenology indicators from VIs are
suffering from mixed-pixel effects\textsuperscript{30}, which can bias the gradients of urban–rural

greenness phenology. Besides, VIs may have noisy signals from soil background, such as

soil color, artificial green building and other non-photosynthetic active materials,

especially in urban areas\textsuperscript{31-33}. On the other hand, originating from the vegetation

photosynthetic pigments, SIF is less sensitive to the soil background\textsuperscript{34-36}.

Our analyses suggest that the urban–rural photosynthetic phenological differences

are mainly controlled by elevated atmospheric CO\textsubscript{2} concentration and daytime

temperature, while the differences of greenness phenology are mostly depending on the

urban size (Fig. 3). Previous studies using dozens of cities at regional scale suggest a

positive correlation between earlier greenup and surface temperature enhancement of

urban areas, such as in eastern North America\textsuperscript{37,38} and China\textsuperscript{21,39,40}. However, our analysis

show that the urban–rural greenness phenological differences are mainly correlated to the

urban size in the Northern Hemisphere, which is in line with a recent study conducted

with thousands of cities in the conterminous United States\textsuperscript{41}. The positive relationship

between urban–rural greenness phenological gradients and urban size (an indicator of

urbanization), may result from the shifts of vegetation percentages and regional climate

conditions induced by urban expansion\textsuperscript{41}. On the contrary, the earlier start and peak of

photosynthesis activity inferred from SIF observations have a significant correlation with

elevated temperature in urban areas (Fig. 4a&b). This discrepancy might partly relate to

the different sensitivity of VIs and SIF to temperature increases, either from satellite

data\textsuperscript{25} or previous site-level study\textsuperscript{42}. More importantly, SIF has a positive correlation with
GPP both in leaf-level and site-level\textsuperscript{19,43,44}, which is a more direct indicator of vegetation physiological status than VIs\textsuperscript{45}. Seasonality of SIF from ground-based measurements\textsuperscript{46}, tower-based observations\textsuperscript{47} and satellite-based data\textsuperscript{25} generally has high correlations with that of GPP. Therefore SIF-based photosynthetic phenology in studies of “urban laboratories” could provide a better proxy of the actual vegetation photosynthetic changes in response to the climate change than VIs, which provide proxies of vegetation greenness.

Using 880 cities, our results confirm that vegetation photosynthesis activities in spring are triggered by daytime temperature, not by nighttime temperature\textsuperscript{8} (Fig. 3). However, the sensitivity of SOS to daytime temperature in this study ($1.55 \pm 0.60$ days per °C) is lower than previous studies for boreal and temperate forests based on longtime satellite VIs or ground observations\textsuperscript{8,9,48-52}. This may reflect the declining warming effects on spring leaf unfolding\textsuperscript{9} and weakening temperature control on the interannual variations of vegetation spring carbon uptake\textsuperscript{53}. The reduced sensitivity of spring leaf unfolding to temperature may partly result from the reduced chilling accumulation in urban areas\textsuperscript{9}, in which the winter temperatures may become insufficiently low to meet the requirement of chilling due to the urban heat island effects. Photoperiod may also influence the warming effects on spring phenology, although its impact remains unclear and is under debate\textsuperscript{5,23,54-55}. We also found that the photosynthetic POS have an earlier trend (about 3.3–6.9 days per decade) in the near decades, which is consistent with the POS trend of $\delta^{13}$C data (about 4.3 ± 2.9 days per decade)\textsuperscript{56}, and are larger than the POS
trends from NDVI data or ground phenology measurements. This phenomenon highlights the advantages of SIF for tracking vegetation seasonal photosynthetic activities and carbon uptake. Our analysis also reveals a delayed end of vegetation photosynthesis in urban areas (Fig. 1). Other than the earlier start of SOS and its response to global warming, our understanding of the drivers for delayed EOS is still limited. Temperature, photoperiod, elevated atmospheric CO₂ and spring phenology were claimed to be associated to this delayed vegetation senescence. Nevertheless, our analysis suggests a pronounced delay in the end of vegetation photosynthesis in urban environments and these delays are highly correlated to the elevated atmospheric CO₂ concentration.

Current studies generally focus on the responses of phenophases to warming, ignoring the importance of additional environmental drivers. From this point of view our analysis highlights that photosynthetic phenological shifts are not only controlled by daytime temperature but also by atmospheric CO₂. CO₂ fertilisation seems to have a large effect on the advancement of photosynthetic activity, particularly under warm and dry conditions; and the delayed end of photosynthesis is mainly attributed to the elevated atmospheric CO₂ rather than temperature, which is consistent with field experiments. The delayed EOS may be because photosynthesis could be sustained for longer period in the absence of sink limitations under elevated atmospheric CO₂ concentrations. Direct evaluations of the future projected phenophase shifts are difficult, however, given a global increase in CO₂ concentration of 16.5 ppm·decade⁻¹ and temperature of...
0.16 °C·decade$^{-1}$ in the past three decades$^{65}$ (1982–2011), our estimates of the prolonged photosynthetic growing seasons ($5.5 \pm 2.1$ days·decade$^{-1}$) are significantly higher than current estimates (2.2 to 3.9 days·decade$^{-1}$) based on long-term satellite vegetation indices$^{66,67}$ and the in situ experimental results based on greenness observations from a recent study$^5$. Our results suggest that the sensitivity of photosynthetic phenology to climate is strikingly higher than that of traditional greenness phenology, and therefore, that the current methods based on satellite VIs and in situ greenness observations are likely to underestimate the extension of carbon sink period under climate change. Crucially, our results show that, with increasing atmospheric CO$_2$, the growing seasons are likely to expand in the next two decades, which in turn might contribute to an increasing trend of the terrestrial carbon sink and generate an important negative feedback in the climate system.

Yet it should be noted that some limitations still remain in our analysis. Landscape configuration, species composition$^{68}$, atmospheric deposition (e.g., nitrogen and phosphorus), air pollutants (e.g., ozone), management practices and hydrological regimes may also affect urban–rural phenological differences. These factors may have complex and to some extent counterbalanced impacts on vegetation photosynthesis in urban environments. For example, urban areas generally receive higher rates of atmospheric nitrogen and phosphorus deposition$^{69}$, which may positively contribute to urban–rural phenological differences (Supplementary Fig. 8b). On the other hand, urban areas typically show higher daytime ozone concentrations that can be detrimental to
photosynthesis, and these urban–rural ozone differences may negatively contribute to the urban–rural phenological differences (Supplementary Fig. 8c).

Besides, vegetation species and human management practices may vary between urban and rural areas; and apart from the temperature and CO₂, water stress indices such as precipitation, vapour pressure deficit (VPD) and soil moisture, may also have influences on the vegetation phenology. Urban–rural phenological gradients in areas with low precipitation are generally more pronounced (Supplementary Fig. 8a), because vegetation in urban areas is likely to be affected by irrigation and thus not limited by water supply. To test whether our results were affected by the irrigation of urban vegetation, we repeated the analysis after excluding the cities in the arid climate zones, assuming that the irrigation effect on urban–rural phenology gradients could be more significant in these areas. Results also showed that the extended photosynthetic seasons in urban areas were both controlled by the elevated temperature and CO₂ (Supplementary Fig. 9a), but with slightly lower sensitivities. Therefore, our predictions of the GSL shifts based on all of the 880 cities may be slightly overestimated with a rate of about 0.8–1.2 days·decade⁻¹ (Supplementary Fig. 9b). Moreover, to verify the robustness of our analysis, we further calculated the phenological differences between the 10-km and 30-km rural buffers and related them with temperature and CO₂ gradients. Results from the gradients between 10-km and 30-km rural buffers showed higher correlations with temperature and CO₂ gradients than those from the original urban–rural gradients (Supplementary Fig. 10). These higher correlations not only confirm the robustness of our analysis, but also suggest that the
confounding factors (e.g., vegetation species, irrigation and nutrient supply) do not affect
the controlling role of temperature and CO₂ in vegetation photosynthetic phenology,
given that the vegetation phenology in 10-km rural buffers are less influenced by these
factors than urban areas. However, these confounding factors can hardly be included in
our analysis due to the lack of high-resolution data at global scale.

The novel insights of this study are derived at large scale from the contrasting
behaviour of plants along the urban–rural gradients. The sharp differences in
environmental conditions along these gradients can represent a unique “natural laboratory”
with different atmospheric CO₂ concentration and temperature that may ultimately inform
on plant behaviours under future climates and atmospheric composition. The
macro-environmental conditions of open urban laboratories are widely reachable in the
globe and can therefore lead to more general and robust assessments of vegetation
responses to key environmental drivers across different environmental conditions in a
global change perspective. Ultimately, our findings shed new light on the behaviour of
plants under global change, help to reduce the uncertainties of terrestrial ecosystems
models74, and increase our understanding of climate–vegetation interactions.
Methods

Urban–rural gradients

We focused our study on urban clusters and their adjacent rural buffers at mid- to high-latitudes in the Northern Hemisphere (NH, ≥30°) from 2015 to 2017 (Supplementary Fig. 1), where vegetation is highly seasonal and sensitive to climate. The extents of the urban areas were mapped using a cluster-based method that estimates optimal thresholds using nighttime stable-light data from the Defense Meteorological Satellite Program/Operational Linescan System (DMSP/OLS). Sensitivity analyses and comparisons with other global urban-area products indicated that this product is reliable and highly accurate. We used this data product (for 2013) instead of extracting urban areas from land-cover data sets, because these cluster-based urban extents clearly define the boundaries between urban and rural areas, regardless of the internal spatial heterogeneity, which is more similar to the real environment that the vegetation experiences. Although the static urban clusters (2013) and our study period (2015–2017) differed by approximately three years, the overall results should not be affected due to almost stable urban clusters in North America and Europe and the slightly increasing urban areas in Asia.

We created a series of buffers extending 10, 20, 30 and 40 km outward from each urban cluster perimeter to select an appropriate threshold for SIF data. Because of the limited spatial coverage of the OCO-2 SIF data, we used an interval of 10 km to ensure that each buffer had a sufficient number of observations. An example of the urban cluster
and its corresponding rural buffers was shown in Supplementary Fig. 11. Pixels that were water body or crops were excluded from this analysis (Supplementary Fig. 11a). Croplands were excluded because their photosynthetic dynamics are strongly affected by human management. We also excluded the pixels in the rural areas which had elevations greater than ±50 m of the average elevation of urban pixels (for both SIF and EVI data, Supplementary Fig. 11b)\textsuperscript{21}. Given that the number of OCO-2 SIF observations per year was low, we opted for the use of SIF data in each urban cluster and its corresponding rural buffers from 2015 to 2017 as one completed phenological cycle. OCO-2 Footprints with viewing zenith angles (VZA) less than 20° in glint and target modes are used\textsuperscript{28}. We selected urban clusters with at least eight SIF observations in both the urban cluster and each corresponding buffer to ensure a successful calculation of phenology. This resulted in a total of 880 urban clusters (Supplementary Fig. 1).

Data

We used the OCO-2 SIF Lite product (B8100) at 757 nm for 2015–2017. OCO-2 is a sun-synchronous polar-orbit satellite launched in July 2014, with an altitude of 705 km and a descending node at approximately 13:30 local time\textsuperscript{18}. OCO-2 leads the “A-Train” satellite constellation with a repeating cycle of approximately 16 days. The instrument collects high-resolution radiance spectra in the O\textsubscript{2}-A band (757–775 nm), which can be used to retrieve fluorescence signals from vegetation. Retrievals based on the in-filling of solar Fraunhofer lines in narrow spectral windows around 757 and 771 nm were conducted using the singular vector decomposition method. The accuracy of single
measurements at 757 nm after a series of bias-correction and quality-control steps is approximately 15-25% of the typical peak values of SIF\textsuperscript{18}. However, because there are dozens of single measurements in each urban cluster and the corresponding rural buffer, most of the noise in the retrieved SIF has been reduced following the $1/\sqrt{n}$ law, which means the precision errors in the average of $n$ samples will get reduced by a factor of $1/\sqrt{n}$\textsuperscript{79}. Moreover, the relative uncertainties of single measurement in the urban clusters and rural buffers are almost the identical (Supplementary Fig. 12); therefore, the retrieval errors of SIF should have not large impacts on the urban–rural phenological patterns. We chose the SIF data at 757 nm because the signals are approximately 1.5-fold greater at 757 than those at 771 nm.

The data for Aqua MODIS EVI collection-6 (MYD13A2; 16-day composite) with a spatial resolution of 1 km for 2015–2017 were used to extract greenness phenology information. The EVI data partially eliminate the effects of canopy background and remain sensitive to small changes in vegetation activity compared to NDVI (normalized vegetation index) data\textsuperscript{20}. Thus, the EVI data are considered to be more appropriate for use in areas with sparse vegetation coverage, such as urban clusters\textsuperscript{21,38}. We used the Aqua EVI data to maintain consistency with the OCO-2 overpass time (both occur at approximately 13:30 local time). To make a comparison, the MODIS EVI data are selected according to the same OCO-2 overpasses. To test whether the observed urban–rural phenological patterns is an artefact of the difference in spatial resolutions between OCO-2 SIF and MODIS EVI, we firstly resampled both SIF and EVI data to a
spatial resolution of 5 km and reproduced the urban–rural phenological differences. The results also demonstrated larger differences of photosynthetic phenology in urban–rural gradients than the differences of greenness phenology (Supplementary Fig. 5) and thus demonstrated the robustness of our analysis.

We obtained the urban–rural XCO₂ gradients using reprocessed Lite files from the OCO-2 product (version 8r) for 2015–2017. The data were bias-corrected using observations from the Total Carbon Column Observing Network (TCCON). OCO-2 also collects high-resolution radiance spectra at the 1.61 and 2.06 μm bands, except for the O₂-A band, which can be used to retrieve XCO₂ based on the Atmospheric CO₂ Observations from Space algorithm. Comparisons with the measurements at TCCON sites demonstrated that the precision of the Lite products was approximately 1.5 ppm.

We used the Aqua MODIS collection-6 land-surface temperature (LST) data set (MYD11A2; 8-day composite), with a spatial resolution of 1 km for 2015–2017 to calculate the urban–rural LST gradient. We chose LST data from the Aqua satellite because its data were acquired at 13:30 and 01:30 local time each day, approximately representing the diurnal and nocturnal temperatures, respectively (i.e., maximum and minimum temperatures). We also used the air surface temperature (AST) data from TerraClimate dataset, with a spatial resolution of 4 km to calculate the urban–rural AST gradient.

We also extracted the mean annual air temperature (2 m above the surface) for each urban cluster from the analytical data set based on both the Global Historical Climatology
Network (version 2) and the Climate Anomaly Monitoring System (GHCN-CAMS), with a spatial resolution of 0.5°. The annual precipitation of each urban area was calculated based on the monthly Integrated Multi-satellite Retrievals (IMERG) data set from global precipitation measurements (GPMs), with a spatial resolution of 0.1°. Digital elevation models (DEM) at a spatial resolution of 30 arc seconds from the GTOPO30 data set and the land-cover data set for 2015 from the European Space Agency (ESA) Climate Change Initiative were also used in this study. We also used the global gridded nitrogen dioxide (NO₂) and ozone (O₃) observations from Ozone Monitoring Instrument (OMI). We calculated the mean LST changes for 2015–2035 at mid- to high-latitudes in the NH (≥30°) from four Earth system models (CSIRO-Mk3.6.0⁸³, GFDL-CM3⁸⁴, GISS-E2-H⁸⁵ and NorESM1-M⁸⁶) within CMIP5. Projected CO₂ concentration changes from 2015 were obtained from the RCP Database. Detailed information on the data sets is presented in Supplementary Table 1.

**Extraction of phenological data**

We used a double-sigmoidal function to fit the annual cycles of the SIF and EVI observations⁸⁷. Choosing an appropriate method to fit noisy SIF data is important because of the wide variation in phenology when estimated with different methods. We chose the double-sigmoidal method for three reasons. First, the speeds of spring leaf out and autumn senescence are not always the same: leaf out is generally faster than senescence⁸⁸. The double-sigmoidal method can identify the actual biophysical dynamics of vegetation by setting two amplitudes for spring and autumn⁸⁷. Second, functional fitting methods
have advantages for estimating phenology with noisy data\textsuperscript{89}. The OCO-2 data are acquired at different time intervals and are relatively noisy, and the number of observations is small. Thus some fitting approaches, such as polynomial fitting, logistic fitting and harmonic analysis, cannot be used or cannot converge to the global optimum. Third, the double-sigmoidal method has been successfully applied to SIF data in a previous study\textsuperscript{33}. The fitting equation is\textsuperscript{36,87}:

\begin{equation}
    y(t) = a_1 + \frac{a_2}{1 + \exp(-d_1(t-b_1))} - \frac{a_3}{1 + \exp(-d_2(t-b_2))}
\end{equation}

where \(y(t)\) represents the observed SIF or EVI for a given day of year (DOY; \(t\)); \(a_1\) represents the value in the winter dormant period; \(a_2\) represents the value at the spring and early summer plateau; \(a_3\) represents the value at the late summer and autumn plateau; \(b_1\) and \(b_2\) are the DOY mid-points of transitions for spring leaf out and autumn senescence, respectively; and \(d_1\) and \(d_2\) are the corresponding slope coefficients of these transitions.

The fitting equation was adapted to our SIF and EVI time series, and the coefficients were optimized using genetic algorithms. A simple weighting scheme was applied to the noisy data. We assigned a weight of two if a central point was within ±50% of the median for a moving window of three points\textsuperscript{33}. A maximum of 20 fitting attempts with different initial values were made until the fitting procedure converged to the global optimum. Each attempt had a maximum of 2000 iterations. The \(R^2\) values of SIF fitting were lower than those of EVI, but most were larger than 0.8 (Supplementary Fig. 13). The \(R^2\) values were generally high for the EVI data. The phenological indicators were then determined
where SOS, POS, EOS and GSL represent the start, peak, end and length of the growing season, respectively. An example of the fitting method and the estimation of phenological indicators is shown in Supplementary Fig. S14a. We excluded some extreme values using a loose threshold to reduce uncertainties and slightly adjusted the thresholds based on previous studies \[^{21,38,41}\] due to the differences between the data and methods. SOSs earlier than the 30\(^{\text{th}}\) or later than the 180\(^{\text{th}}\) DOY, and EOSs earlier than the 240\(^{\text{th}}\) or later than the 350\(^{\text{th}}\) DOY, were thus excluded from our analysis. To test whether our results were affected by the weighting scheme, we also calculated the phenological indicators after changing the moving-window and without using the weighting scheme. Results showed no significant differences compared to the original method (Supplementary Fig. S14 b-c).

The urban–rural phenological gradients were also evident using these different weighting schemes (Supplementary Fig. S14 d-e).

**Conversion of urban–rural XCO2 gradients to surface CO2 gradients**

The XCO2 data are column-averaged CO2 mixed ratios and differ in magnitude from CO2 concentrations near the surface. Therefore, in order to investigate the effect of CO2
fertilization on vegetation phenology, we need to convert the urban–rural XCO\(_2\) gradients to surface CO\(_2\) gradients. Although atmospheric transport models would be the ideal approach to fulfill this purpose, there are still many precluding issues. Firstly, high-spatial resolution prior fluxes of CO\(_2\), including the anthropogenic emissions and terrestrial carbon uptake, as well as the high-resolution meteorological data (wind speed and wind direction), still have large uncertainties, especially in urban areas with high-variable emission sources (such as traffic pollution) and high degrees of surface heterogeneity\(^{90,91}\). Secondly, as one of the main factors that affect the variations of surface CO\(_2\) concentration in finer scales, the heterogeneity of vertical profile in urban areas induced by buildings can hardly be accurately estimated and illustrated\(^{92}\). Thirdly, continuous high-spatiotemporal ground and satellite CO\(_2\) measurements are still insufficient to provide accurate constraints and evaluations for atmospheric transport models to simulate the high-spatial resolution surface CO\(_2\) concentrations at large scales\(^{93}\). Therefore, global near-surface CO\(_2\) concentrations from atmospheric transport models or flux-inversion systems generally have relatively low spatial resolutions\(^{94}\), which cannot meet our needs for deriving urban–rural gradients at large scales. Statistical methods are therefore more appropriate for converting XCO\(_2\) gradients to surface CO\(_2\) gradients.

We used two approaches to determine the conversion factors. First, we used a near-surface CO\(_2\) data set with a comprehensive spatial coverage. The data were obtained in Shanghai during April and May of 2014 and covered the entire urban area, with a total of 172 sample points\(^{95}\) (Supplementary Fig. 15). The slopes of the near-surface CO\(_2\)
measurements and OCO-2 XCO\textsubscript{2} observations in the same city were calculated (Supplementary Fig. 16a-b). The conversion factor could then be obtained (\( K = 21.2 \)).

Second, we collected a number of urban–rural surface CO\textsubscript{2} gradients from previous studies (Supplementary Table 2) and then calculated the XCO\textsubscript{2} gradients of these urban clusters and compared them via linear regression (Supplementary Fig. 16c), which indicated that the conversion factor was approximately 28.5. These data from previous literatures have an average of seven years gap with the satellite observations, and thus the observations of urban–rural surface CO\textsubscript{2} gradients may be lower than those of present, which possibly leads to a higher estimation of the K factor. Therefore, we used a K factor of 25, which is the average value of these two approaches. Then we converted the urban–rural XCO\textsubscript{2} gradients to surface CO\textsubscript{2} gradients through this conversion factor. This conversion factor was derived via statistical methods that may have some uncertainties. For example, the K factor derived from the first approach was 21.2 ± 8.3; while that from the second approach was 28.5 ± 9.5 (mean ± standard error). To test the robustness of our results according to different K values, we repeated our analysis using a wide range of K factors (from 19 to 30), which was the intersection of ranges of the K factors estimated from these two approaches. Results showed that the partial correlations between urban–rural phenological gradients and CO\textsubscript{2} gradients were not affected by K values, given that this conversion factor was linear (Supplement Fig. 17a). Although the predicted GSL had a declining trend when the K was increasing (Supplement Fig. 17b), our predicted GSL shifts (5.9–11.4 days·decade\textsuperscript{−1}) based on a K factor of 25 were
comparable to the average value of these shifts. These results suggested that the joint control of elevated CO$_2$ and temperature on urban–rural photosynthetic phenological gradients was robust across different K values.

**Analysis**

The phenological differences, LST gradients and CO$_2$ gradients between urban and rural areas for each city were first calculated as:

$$\Delta P = P_{urban} - P_{rural}$$  \hspace{1cm} (3)

where $\Delta P$ represents the urban–rural gradients for the phenological indicators (SOS, POS, EOS and GSL), LST and CO$_2$ concentration; and $P_{urban}$ and $P_{rural}$ represent these values in urban clusters and their corresponding rural buffers, respectively. The LST differences included the mean spring LST (January to May, corresponding to SOS), mean summer LST (June to August, corresponding to POS), mean autumn and winter LST (September to December, corresponding to EOS) and mean annual LST (corresponding to GSL)\textsuperscript{38}. Due to the limited OCO-2 observations, we used the whole year XCO$_2$ observations and the conversion factor (K) to derive the urban–rural CO$_2$ gradients. The differences in photosynthetic (SIF) and greenness (EVI) phenology along the urban–rural gradients for different rural buffers (i.e., 10, 20, 30 and 40 km) were calculated (Supplementary Fig. 4). Previous studies have shown that the mean footprint of urban areas on phenology was about 20–25 km, which should be able to reflect the background vegetation phenology\textsuperscript{31,38,96}. In this analysis, we found that the largest urban–rural phenological differences occurred between urban clusters and 30-km rural buffers. Therefore, we
therefore used the 30-km rural buffers as representatives in the subsequent analyses.

The spatial distribution of photosynthetic phenology differences based on latitude, mean annual air temperature and precipitation were then analysed. We also analysed the phenological differences in different climate zones based on the Köppen–Geiger climate zones classification (http://people.eng.unimelb.edu.au/mpeel/koppen.html). To determine the main controlling drivers of urban–rural phenological gradients, we determined the partial correlations of $\Delta P$ with latitude, longitude, urban size, mean annual air temperature, annual precipitation, CO$_2$ gradient ($\Delta$CO$_2$) and LST gradient ($\Delta$LST). The partial correlation (two-tailed) of each factor was determined while controlling the other factors. In order to reduce the stochastic error, the LST and CO$_2$ gradients are binned every 0.15°C and 1.5 ppm, respectively. Then we determined the main factors controlling each phenological indicator by analysing the associations between urban–rural phenological gradients with temperature and CO$_2$ enhancements. Furthermore, we derived their sensitivities with a forward stepwise regression model (Supplementary Table 3). This method automatically repeats the procedures of forward selection and backward elimination. In each step, an explanatory variable is considered to either add or subtract from the set of variables based on a sequence of $F$ tests. Finally, we estimated the near-term projected shifts in photosynthetic phenology by multiplying the sensitivities with LST and CO$_2$ concentration predictions during 2015–2035 based on four RCP scenarios (RCP 2.6, 4.5, 6.0 and 8.5).

Finally, we analysed the uncertainty of projected phenophase shifts as a consequence
of using LST other than air surface temperature (AST) to characterise the urban–rural
temperature gradients. Vegetation phenology theoretically should respond to AST more
than to LST. As shown in previous studies on the impact of land cover on temperature\textsuperscript{97},
the spatial gradients of AST are likely smaller than that of LST (Supplementary Fig. 18a),
which may translate in a higher sensitivity of GSL to AST than to LST (Supplementary
Fig. 18b). Therefore, projected shifts of GSL based on urban–rural AST gradients might
be larger than that based on LST gradients (Supplementary Fig. 18c; approximately
0.5–0.8 days·decade\textsuperscript{−1}). However, current high-resolution AST datasets are generally
based on observations from weather stations, which cannot fully capture the small scale
urban–rural heterogeneity because of the low density of stations. Due to the limitation in
the current AST datasets, analysis based on this latter variable may actually have larger
uncertainties than those based on LST and will need more investigations in the future.

\textit{Code availability}

The codes used to estimate the phenological indicators in this study are available at

https://drive.google.com/drive/folders/1yzcoRAjjubiLDqlg6zbLUCfE_m1mHAsL?usp=s

\textit{Data availability}

OCO-2 SIF and XCO\textsubscript{2} data are available at https://disc.gsfc.nasa.gov/. MODIS EVI
and LST data are available at https://ladsweb.modaps.eosdis.nasa.gov/. Precipitation data
can be obtained from https://pmm.nasa.gov. GHCN-CAMS air temperature data are
available at https://www.esrl.noaa.gov. CCI Land cover data are available at

References


Peng, S. *et al.* Surface urban heat island across 419 global big cities.


Chuine, I., Morin, X. & Bugmann, H. Warming, photoperiods, and tree phenology.


Sun, Y. *et al.* OCO-2 advances photosynthesis observation from space via


Marchin, R. M., Salk, C. F., Hoffmann, W. A. & Dunn, R. R. Temperature alone does not explain phenological variation of diverse temperate plants under


Fisher, J. B., Huntzinger, D. N., Schwalm, C. R. & Sitch, S. Modeling the


Collier, M. *et al.* in *International Congress on Modelling and Simulation–MODSIM*.


97 Alkama, R. & Cescatti, A. Biophysical climate impacts of recent changes in
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Author contributions

Y.G.Z. designed the research; S.H.W. performed the analysis; S.H.W., Y.G.Z. and W.M.J. drafted the paper; J.P., and A.C. contributed to the interpretation of the results and to the writing of the paper; A.H., Y.Y.Z. and Y.S.F. contributed to the writing of the paper; Y.Y.Z. and M. L. provided the data.

Competing interests

The authors declare no competing interests.
Fig. 1. Mean urban–rural phenological differences based on SIF and EVI. SOS, start of
growing season; POS, peak of growing season; EOS, end of growing season; GSL, length
of growing season. The operator Δ represents the differences in phenological indicators
between urban areas and rural buffers (e.g., ΔSOS = SOS\text{urban} − SOS\text{rural}). The error bars
represent standard errors of the mean (n = 880).

Fig. 2. Spatial distributions of ΔSOS (a), ΔPOS (b), ΔEOS (c) and ΔGSL (d) for SIF (n =
880). The first column represents the urban effects on phenological metrics for various
urban clusters. The second column represents phenological differences based on
latitudinal profiles (the shaded areas represent the standard errors of the mean); whereas
the third column shows the average metrics for various climatic backgrounds (mean
annual air temperature and annual precipitation).

Fig. 3. Partial correlations of SIF (a) and EVI (b) urban–rural phenological differences
(ΔSOS, ΔPOS, ΔEOS and ΔGSL) with explanatory variables. Lat: latitude; Lon: longitude;
Size: log 10 of the urban size; Air T: mean annual air temperature; Pre: mean annual
precipitation; ΔCO2: urban–rural CO2 difference; ΔT\text{day}: daytime urban–rural land surface
temperature difference; ΔT\text{night}: night-time urban–rural land surface temperature difference;
SOS: start of growing season; POS: peak of growing season; EOS: end of growing season;
GSL: length of growing season. *: p < 0.05; **: p < 0.01 (n = 880).

Fig. 4. Associations between elevated temperature (a–d), CO2 (e–h) and urban–rural
photosynthetic phenological gradients. ΔCO2, urban–rural CO2 gradient; ΔLST\text{day},
urban–rural gradient of daytime LST. The LST and CO2 gradients are binned every
0.15°C and 1.5 ppm, respectively; each dot represents a bin. The solid lines indicate significant trends and the shaded areas represent the 95% confidence intervals, and p values represent the significance (Student’s t-tests, n = 880).

**Fig. 5.** Projected shifts in photosynthetic phenology during the next two decades. Sensitivities of photosynthetic phenology to temperature (a) and CO₂ (b). The error bars represent standard errors of the mean. c–f, Shifts of photosynthetic SOS, POS, EOS and GSL from 2015 to 2035, as calculated from the sensitivities shown in a–b and LST and CO₂ concentration predictions during 2015–2035 from four “Representative Concentration Pathway” (RCP) scenarios. The shaded areas represent the standard errors.

**g,** Projected shifts of photosynthetic phenology during the next two decades in per decade (days·decade⁻¹). The negative values represent the advances of SOS and POS, and positive values represent a delayed EOS and a prolonged GSL. The error bars represent standard errors of the mean.