

## Manuscript Template

1  
2 **FRONT MATTER**

3  
4 **Title**

5 Combining solar-induced chlorophyll fluorescence and optical vegetation indices to better  
6 understand plant phenological responses to global change

7  
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19  
20 **Abstract**

21 Recent advances in the satellite retrieval of solar-induced chlorophyll fluorescence (SIF) provide  
22 new opportunities for understanding the phenological responses of ecosystems to global climate  
23 change. Due to the strong link between SIF and plant gross photosynthesis, phenological events  
24 derived from SIF represent the seasonal variation of ecosystem functioning (photosynthetic  
25 phenology) and differs from phenologies derived from traditional vegetation indices (VIs). We  
26 provide an overview of recent advances in remotely sensed photosynthetic phenologies, with a  
27 focus on their driving factors, their impact on the global carbon cycle, and their relationships with  
28 VI-derived land surface phenology metrics. We also discuss future research directions on how to  
29 better use various phenological metrics to understand the responses of plants to global change.

30  
31 **MAIN TEXT**

32  
33 **1. Background**

34  
35 Plant phenology, i.e. recurrent events in plant life cycles, has changed substantially during the past  
36 decades (Körner and Basler, 2010). The timing of spring phenological events, e.g., budburst and  
37 leafing, have continuously advanced based on a large number of in situ phenological observations,  
38 but the date of foliar senescence has mostly been delayed (Peñuelas and Filella, 2001). A consensus  
39 has been reached that these changes are mostly caused by global warming, which has increased the  
40 accumulation of heat in spring and alleviated cold stress in autumn, but the underlying mechanisms  
41 remain unclear (Estiarte et al., 2022; Estiarte and Peñuelas, 2015; Fu et al., 2015; Piao et al., 2019;

1 Walther et al., 2002; Zhang, 2022). These changes have nevertheless extended the growing season  
2 and altered the rate of vegetation green-up for many ecosystems (Cleland et al., 2007). Such canopy  
3 structural changes not only affect the seasonal growth of vegetation and the sequestration of carbon  
4 in terrestrial ecosystems (Barichivich et al., 2013), but also alter Earth's surface processes and  
5 energy balances (Peñuelas et al., 2009), both contributing to the complexity of future climate change  
6 projections (Bonan and Doney, 2018).

7  
8 Remote sensing has long been used to characterize phenology at the ecosystem scale (Schwartz,  
9 1998). Satellite-derived vegetation indicators, unlike traditional observations of phenological  
10 events for individual plants, depict seasonal changes of canopy greenness, often known as land  
11 surface phenology (Ma et al., 2022). The normalized difference vegetation index (NDVI), which  
12 has the longest global continuous records since 1981 (Pinzon and Tucker, 2014), is the most  
13 commonly used vegetation indicator. Multiple metrics can be derived from smoothed curves  
14 generated from repeated satellite observations for each pixel, e.g., green-up, maturity, peak,  
15 senescence, dormancy, growing season length, and amplitudes of seasonal variation (Ganguly et  
16 al., 2010). Trend analyses for these metrics provide multi-dimensional descriptions of vegetation  
17 phenological changes (Buitenwerf et al., 2015). Although observations from various satellites may  
18 differ in the magnitude of the changes (Zhang et al., 2013), advanced green-up and delayed  
19 senescence have been widely observed based on multiple VI data sets, consistent with the results  
20 from long-term in situ phenological networks (Jeong et al., 2011; White et al., 2009).

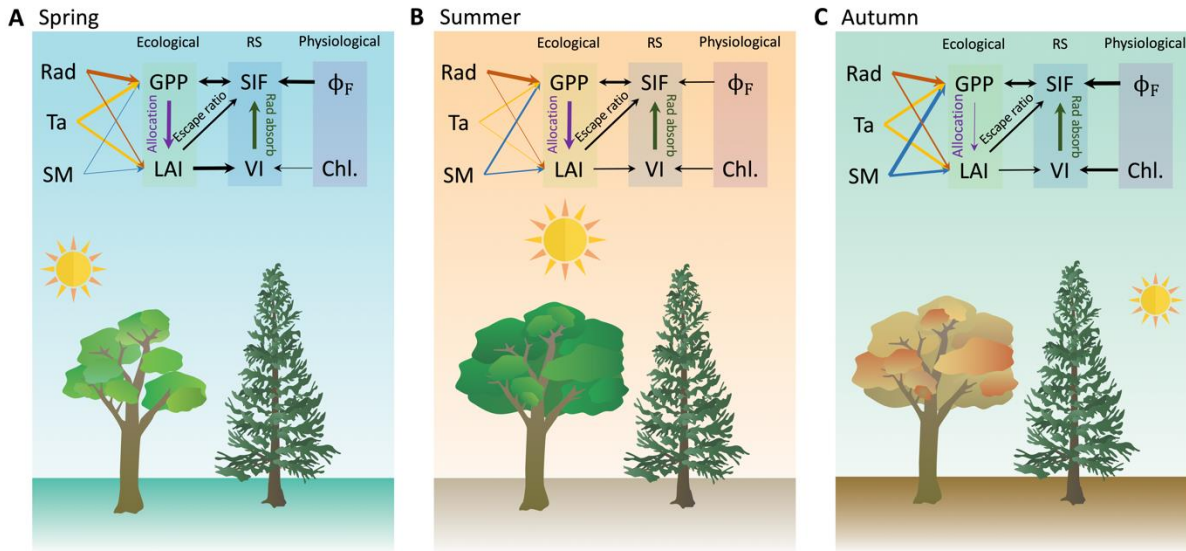
21  
22 Solar-induced chlorophyll fluorescence (SIF) has become increasingly used for phenological  
23 analyses since its successful retrieval from satellite platforms (Frankenberg et al., 2011, p. 20; Jeong  
24 et al., 2017; Joiner et al., 2014). SIF is a small amount of the energy (usually less than 2%) emitted  
25 by foliar chlorophyll during the photosynthetic light reaction. After a photon is absorbed by a  
26 chlorophyll molecule, it can either be used for photochemistry, dissipated as heat, reemitted as  
27 fluorescence, or decay during these processes (Porcar-Castell et al., 2014). The relationship  
28 between SIF and optical vegetation indicators can be described as:

$$29 \quad \text{SIF} = \text{PAR} \times \text{fPAR}_{\text{chl}} \times \phi_{\text{F}} \times \text{f}_{\text{esc}} \quad (1)$$

30 where PAR,  $\text{fPAR}_{\text{chl}}$ ,  $\phi_{\text{F}}$ , and  $\text{f}_{\text{esc}}$  represent photosynthetically active radiation, the fraction of  
31 PAR absorbed by the canopy chlorophyll, which is strongly correlated with the VIs, the efficiency  
32 of fluorescence emission, and the fraction of SIF emitted by leaves that can be ultimately detected  
33 by a satellite.

34  
35 SIF has been demonstrated to strongly correlate with vegetation photosynthesis at large spatial and  
36 temporal scales due to the shared component of the absorption of solar radiation by canopy  
37 chlorophyll, and the strong coupling between the subsequent partitioning of energy into  
38 photochemistry and fluorescence (Li et al., 2018; Liu et al., 2022; Magney et al., 2020; Porcar-  
39 Castell et al., 2021; Sun et al., 2017; Zhang et al., 2016; Z. Zhang et al., 2023). Consequently, land  
40 surface phenology derived from SIF differs from phenology based on VIs (Fig. 1). From the  
41 perspective of ecology, NDVI and other greenness-based indices represent the seasonal variation  
42 of canopy development, but SIF represents the variations of ecosystem photosynthesis (Yang et al.,  
43 2022). From the perspective of plant physiology, variations in canopy greenness depend on both  
44 changes in foliar area and the concentrations of foliar pigments; SIF additionally responds to  
45 various environmental stresses that downregulate fluorescence efficiency from its normal values.  
46 From the perspective of remote sensing, VIs are calculated based on surface reflectance, which is  
47 affected by the characteristics of the canopies and the atmospheric conditions, whereas SIF  
48 retrievals depend not only on the total amount of fluorescence emission from all leaves, but also on  
49 the radiative transfer within canopy that determines the fraction of total SIF that can escape from  
50 the canopy to be observed by a satellite. These factors are interrelated, and their dependencies are

1 seasonally variable due to canopy development and climatic regulation (Fig. 1). In this perspective,  
 2 to clarify the difference between these two types of land surface phenology metrics, we term SIF  
 3 and VI based phenologies as photosynthetic phenology and greenness phenology, respectively.  
 4



5  
 6 **Fig. 1.** Schematics of the seasonal variations of environmental factors, SIF, vegetation indices  
 7 (VIs), and their interactions for (A) spring, (B) summer, and (C) autumn. Line thickness indicates  
 8 the strength of the effect, which varies for each season. Rad, solar radiation; Ta, air temperature;  
 9 SM, soil moisture; GPP, gross primary production; LAI, leaf area index; SIF, solar-induced  
 10 chlorophyll fluorescence; VI, vegetation index;  $\Phi_F$ , fluorescence efficiency; Chl., chlorophyll  
 11 concentration.

12  
 13 Using SIF to retrieve vegetation photosynthetic phenology, however, faces multiple issues. First,  
 14 satellite SIF data have large uncertainties for individual retrieval, which needs to be further reduced  
 15 by averaging multiple observations over either space or time. Second, the sampling is mostly sparse  
 16 over space or time (Sun et al., 2018). For example, among the widely used instruments capable of  
 17 SIF retrievals, Global Ozone Monitoring Experiment-2 (GOME-2) has 1-4 repeated observations  
 18 for each month within a grid; Orbiting Carbon Observatory-2 (OCO-2) observations are based on  
 19 swaths and do not provide spatially contiguous coverage; and TROPospheric Monitoring  
 20 Instrument (TROPOMI) has a higher observation frequency and contiguous global coverage  
 21 compared to the other two, but the spatial resolution is still too coarse for fine-scale analysis. Third,  
 22 most SIF data sets do not have long-term records, which is critical for the analysis of phenological  
 23 trend. To solve these issues, methods have been proposed that use machine learning to reconstruct  
 24 SIF data based on surface reflectance, solar radiation, and other environmental factors (Gentine and  
 25 Alemohammad, 2018; Li and Xiao, 2019; Y. Zhang et al., 2018a). These methods differ in the  
 26 target SIF data set, explanatory variables, machine-learning algorithms, and selection of training  
 27 samples. The performance of these models are similar, and the relationships between  
 28 photosynthesis and these reconstructed SIF data are strong (Shekhar et al., 2022). Alternatively,  
 29 some attempts have been made using cumulative distribution frequencies (CDF) matching to  
 30 concatenate SIF data from various satellites. Combined with the downscaling of light-use-  
 31 efficiency-guided models, long-term, high-resolution SIF data sets can be generated (Wang et al.,  
 32 2022). Most of these data sets overcome the issue of large uncertainties and the limited spatial and

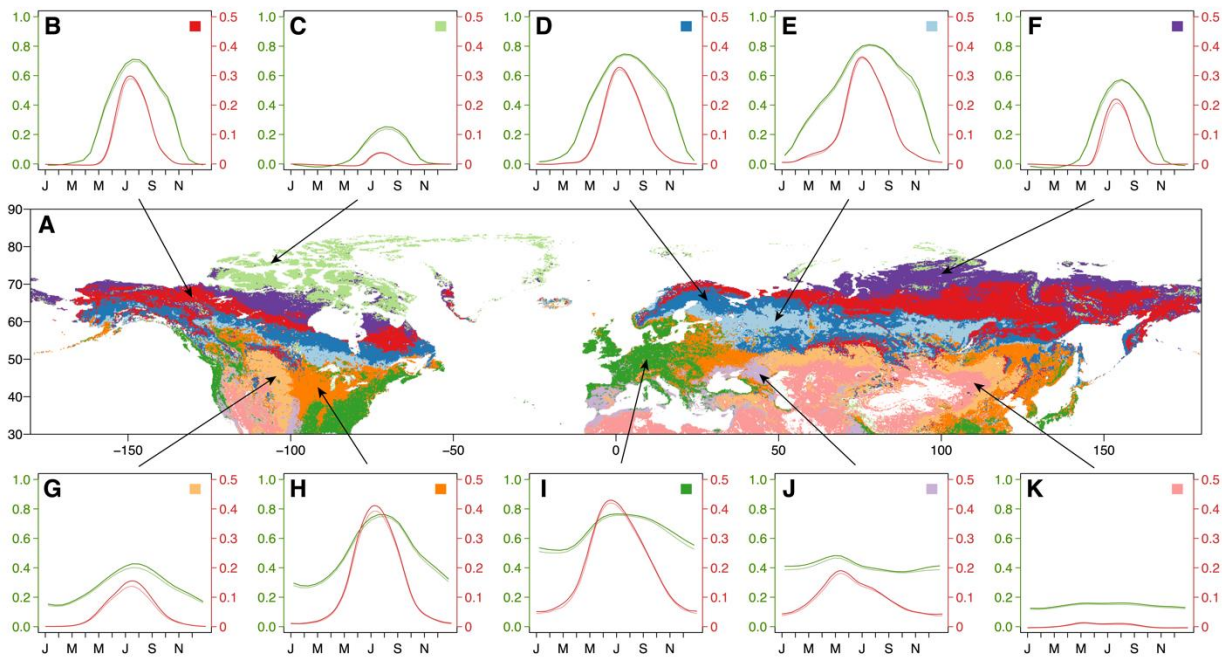
1 temporal coverage of the original SIF data sets, so are suitable for deriving vegetation  
2 photosynthetic phenology (Zhang et al., 2020a). Comparisons of phenologies derived from SIF and  
3 phenologies derived from VIs have shed new light on global change ecology, plant physiology and  
4 terrestrial carbon cycle (Jeong et al., 2017; Yang, 2022; Zhang et al., 2020a; Zhao et al., 2022). In  
5 this perspective, we will (1) demonstrate the differences between photosynthetic and greenness  
6 phenology using remote sensing data, (2) elaborate how environmental factors contribute to the  
7 differences between these two phenological metrics, and (3) propose future research directions  
8 utilizing these two metrics to understand climate change impact on terrestrial ecosystems. Although  
9 we mostly focus on the northern mid to high latitude in this perspective, the mechanisms should  
10 also apply to the south hemisphere.

## 11 **2. General patterns of the phenological metrics derived from SIF and NDVI data**

12 Phenologies derived from SIF clearly differ from those derived from NDVI (Fig. 2). Photosynthesis  
13 has a strongly seasonality for most ecosystems in the Northern Hemisphere, with SIF close to zero  
14 during the boreal winters. NDVI, though, is highly spatially variable in the non-growing season.  
15 For example, winter NDVI at mid- to low latitudes is high for more-mesic regions in Europe,  
16 eastern USA, and southern China and Japan (Fig. 2D) and is lower in arid regions and croplands  
17 (Fig. 2H-J). Snow cover can be a major issue that decreases winter NDVI for ecosystems at high  
18 northern latitudes (Fig. 2E, G, and K). Most mid-latitude forest and cropland ecosystems are greener  
19 and more productive (Fig. 2B, C, D, G, and I) than cold arctic regions, arid central Asia, and western  
20 USA (Fig. 2E, F, H, J, and K). The higher the NDVI, the higher the SIF during peak months.

21 The timing of phenological events derived from SIF and NDVI also differs greatly.  
22 Photosynthetically active seasons derived from SIF are shorter than the growing seasons derived  
23 from NDVI for most ecosystems, especially at northern high latitudes (Fig. 2B, C, E, G, and K).  
24 Most ecosystems also have a later peak of canopy greenness than the peak of photosynthesis, with  
25 exceptions in some arid regions at low latitudes (Fig. 2F and J). These phenological differences  
26 have been confirmed by previous studies (Dannenberget al., 2020; Yang et al., 2022; Zhao et al.,  
27 2022).

28 Green-up has advanced in many ecosystems, often accompanied by higher maximum greenness. In  
29 comparison, the delay of dormancy is less evident, except for dry temperate ecosystems (Fig. 2H).  
30 Similarly, the start of the photosynthetically active season has also advanced, but the end of  
31 photosynthesis has been delayed only a little. Differences exist, for example, in the mesic temperate  
32 ecosystems, where the delay is much longer for greenness than photosynthesis. Peak greenness and  
33 photosynthesis have generally advanced, but the differences between the two peak timings are  
34 increasing (Park et al., 2019; Zhao et al., 2022). Changes of both phenological metrics reflect an  
35 altered plant growth under global warming and associated changes in terrestrial carbon cycle  
36 (Richardson et al., 2010).



1 **Fig. 2.** Patterns of vegetation seasonality and its changes represented by both MODIS NDVI and  
 2 contiguous SIF (CSIF) (Zhang et al., 2018a). (A) Ten regions that have similar seasonality and  
 3 changes for northern mid- to high latitudes (>30°N), clustered using the K-means method based on  
 4 the mean seasonal patterns for the first two decades of the 21<sup>st</sup> century. (B-K) Seasonal patterns of  
 5 NDVI (green, left axis) and CSIF (red, right axis) for the 10 regions, with lighter line colors  
 6 indicating mean seasonal patterns for the first decade, and darker colors indicating mean seasonal  
 7 patterns for the last decade.  
 8  
 9

### 10 3. Factors contributing to the differences in VI- and SIF-based phenological metrics

11 The relationship between VI- and SIF-based phenological metrics is affected by many factors, and  
 12 understanding their differences in both absolute values and trends can provide insights into the  
 13 responses of plants to global climate change. On one hand, from the light use perspective, the  
 14 coverage of a green canopy determines the fraction of light that can be absorbed, and early foliar  
 15 green-up may lead to early photosynthesis. Plant photosynthesis, however, is additionally affected  
 16 by other environmental factors, e.g., temperature, radiation, water, and nutrients. Seasonal  
 17 variations of these factors can strongly influence the seasonality of photosynthesis (Fig. 1). On the  
 18 other hand, from the carbon allocation perspective, deciduous plants rely on both photosynthetic  
 19 carbon gain and carbon storage in the previous season to grow leaves and develop canopies, and  
 20 more photosynthesis also increases the rate of canopy green-up and VI changes (Cabon et al., 2022;  
 21 Meng et al., 2023). These interactions are also mediated by the local environment. Below, we  
 22 discuss the main factors that contribute to the discrepancies between these metrics.  
 23  
 24

#### 25 *Solar radiation*

26 Seasonal changes of radiation or daylength are important environmental cues for plant phenological  
 27 events (e.g., green-up, senescence, and dormancy) (Meng et al., 2021; Way and Montgomery, 2015;  
 28 Zhang et al., 2020a). They are also first-order factors that drive seasonal photosynthetic variation  
 29 (Monteith, 1972). Lower solar elevation angles in spring and autumn induce an additional limitation  
 30 of radiation on photosynthesis, which can explain the generally shorter photosynthetically active  
 31

1 season than the growing season based on greenness. Green-up is usually closer to the summer  
2 solstice than to senescence, so light limitation is stronger in the autumn than the spring.

3  
4 Solar radiation affects SIF independently from changes in vegetation canopy, whose effect in spring  
5 and autumn can be characterized as the relative importance of radiation compared to other  
6 components in driving the changes of the photosynthetically active season. For example, in boreal  
7 evergreen ecosystems with small seasonal variation of canopy greenness and large seasonal  
8 variation of radiation, solar radiation mostly drives the seasonal variations of SIF and  
9 photosynthesis, and the radiation limitation is strong. While for temperature ecosystems where  
10 canopy greenness exhibited greater seasonal variation than the solar radiation, the radiation  
11 limitation is weak. SIF-based photosynthetically active seasons have smaller variations compared  
12 to the variations of the growing season derived from VI. This difference is more evident in the  
13 autumn than the spring, which has been attributed to a stronger limitation of radiation in the autumn  
14 (Zhang et al., 2020a).

15  
16 The stronger limitation of radiation in the autumn can have a large impact on the responses of  
17 ecosystems to warming (Descals et al., 2022; Zhang et al., 2020a). Canopy greenness may increase  
18 during warmer autumns, but such an increase may have limited effects on the enhancement of  
19 ecosystem photosynthesis due to the limitation of radiation. A warmer autumn also increases both  
20 autotrophic and heterotrophic respiration. Whether a warmer autumn can lead to a larger uptake of  
21 ecosystem carbon thus depends on the balance between the warming-induced increase in  
22 photosynthesis and the increase in respiration, in which radiation plays a critical role. Zhang et al.  
23 (2020a) used eddy-covariance data sets combined with SIF- and VI-derived limitations of radiation  
24 to demonstrate that the greater the limitation of radiation, the stronger the release of carbon during  
25 warmer autumns.

26  
27 Future global warming is not expected to shift the seasonal variation of radiation, but the limitations  
28 of radiation on plant photosynthesis may increase, because warming-induced extensions of the  
29 growing season would advance and delay vegetation activities in spring and autumn, respectively.  
30 Earth system models have also identified this increase, with stronger magnitudes for higher latitudes  
31 (Zhang et al., 2020a). This increase may also account for the observed decrease in the sensitivity of  
32 spring leaf unfolding to temperature in recent decades (Fu et al., 2015). Descals et al., (2022) have  
33 more recently confirmed that radiation was a major factor limiting photosynthetic activity that  
34 constrained the phenological response to temperature during the end of the growing season. In  
35 contrast, the start of carbon uptake is generally highly sensitive to temperature but is not constrained  
36 by radiation at the hemispheric scale.

### 37 **Temperature**

38 Temperature can strongly limit photosynthesis and SIF, especially during the winter for evergreen  
39 ecosystems. Canopy greenness has limited variation in these ecosystems, and low temperatures  
40 inhibit vegetation photosynthesis even when radiation and other resources are available.  
41 Photochemistry (photosynthesis), fluorescence, and nonphotochemical quenching (NPQ) compete  
42 for the energy absorbed by chlorophyll, but decreased partitioning of energy to photochemistry  
43 does not necessarily increase fluorescence, which has been widely observed in boreal evergreen  
44 ecosystems and is due to a strong increase in sustained NPQ (Kim et al., 2021; Míguez et al., 2015;  
45 Porcar-Castell, 2011). Unlike reservable NPQ, which is associated with diurnal light saturation,  
46 sustained NPQ varies at weekly or monthly timeframes and provides an important energy outlet  
47 during winter dormancy (Raczka et al., 2019). Such mechanisms lead to a strong seasonal  
48 covariation between SIF and photosynthesis for conifers.



1 Although changes to canopy greenness are limited in evergreen ecosystems, snow cover in the  
2 winter can strongly decrease NDVI, causing a “fake” green-up and dormancy signal that  
3 corresponds to the dynamics of snow cover (Wang et al., 2013). These “fake” green-up and  
4 dormancy signals may, in some cases, correspond to the start and end of photosynthesis, due to the  
5 abrupt changes in air temperature associated with the melting and accumulation of snow cover.  
6 Such signals, however, are unreliable in other ecosystems and do not represent the actual changes  
7 in canopy greenness. Snow cover also affects canopy light absorption and the radiative transfer of  
8 fluorescence within canopies, but the effect of thermal stress on fluorescence efficiency is  
9 considered the most influential factor (Kim et al., 2021; Magney et al., 2019). Some recent studies  
10 have proposed new VIs that either track the seasonal changes of foliar chlorophyll concentration or  
11 are robust to the effects of snow cover, but the differences in phenological metrics derived from  
12 these indices and SIF have not been systematically evaluated and are not likely to be able to track  
13 physiological thermal stress (Huang et al., 2021; Wang et al., 2017). Considering plant phenological  
14 responses often lag behind the rate of warming, leaves would develop at higher temperatures with  
15 relieved cold stress on photosynthetic physiology. This lag has led to increased photosynthesis in  
16 spring and faster canopy development in recent decades (Park et al., 2020).

17  
18 In addition to cold stress, plants also have optimal temperatures for various enzymes and  
19 photochemical reactions. Temperatures above these optima can adversely affect photosynthesis,  
20 which may deviate the peak of photosynthesis from the peak of greenness in some ecosystems when  
21 peak canopy greenness corresponds to a temperature higher than optimal for photosynthesis (Huang  
22 et al., 2019). A recent study demonstrated that this effect could be important for forest ecosystems  
23 (Zhao et al., 2022). Extremely high temperatures may also temporally deviate SIF from canopy  
24 greenness, but this is often associated with water deficits, which we discuss in the next section.

## 25 26 **Water**

27 Water deficits can also impair photosynthesis from its potential maximum. The limitation of water  
28 mostly affects the timing of the peak and end of photosynthesis, especially for arid and semi-arid  
29 ecosystems (Hufkens et al., 2016). Water deficits in both the soil and atmosphere reduce stomatal  
30 conductance, the foliar water potential, and the transport of xylem water, all of which increase NPQ  
31 and decrease photochemical and fluorescence efficiencies (Gupta et al., 2020). These physiological  
32 limitations can be ephemeral and can be alleviated after a rain or heatwave, but they can also be  
33 long-lasting and cause substantial damage to canopy greenness (Schwalm et al., 2017). Water stress  
34 is nevertheless likely to more strongly limit the SIF-based photosynthetically active season than the  
35 greenness-based growing season, because plant physiological processes respond faster than the  
36 changes to canopy structure (Zhang et al., 2020b). Water stress can be strong during the latter half  
37 of the growing season, so its limitation on plant photosynthesis likely advances peak  
38 photosynthesis. Such a mechanism is important in grassland and induces a large asynchrony  
39 between peak photosynthesis and peak greenness (Zhao et al., 2022).

40  
41 Global warming and CO<sub>2</sub> fertilization have contrasting effects on soil moisture through either  
42 increased evapotranspiration induced by greening, or reduced foliar transpiration due to stomatal  
43 closure (Berg, 2021; Zhang et al., 2022). However, a stronger limitation of moisture has been  
44 reported, particularly for foliar senescence in autumn (Wu et al., 2022) and the end of  
45 photosynthesis (Zhang et al., 2020b). An extended growing season, enhanced vegetation activity,  
46 and warming-induced atmospheric dryness all contribute to an increase in water consumption by  
47 plants and stronger water limitation, but the differences in sensitivity between SIF and the VIs still  
48 need further investigation.

## 49 50 **Nutrients**

1 Foliar nutrient concentrations also play a role in accounting for the differences in canopy greenness  
2 and photosynthesis, but their effect depends on the nutrient. For example, a lack of phosphorus may  
3 inhibit the development of foliage and delay the peak timing of canopy greenness. Nitrogen, as an  
4 important element for the synthesis of photochemical enzymes, can have a more direct influence  
5 on fluorescence and photosynthesis. A recent study reported a limited contribution of nitrogen to  
6 the seasonal mismatch between photosynthesis and canopy structure (Zhao et al., 2022), perhaps  
7 because nitrogen concentration varies little seasonally and the seasonalized variation of canopy  
8 development and nitrogen concentration is synchronized. Nutrient concentrations play a  
9 predominant role in regulating canopy development and the timing of peaks between  
10 photosynthesis and canopy greenness, especially for forest ecosystems. Such a late canopy  
11 development could potentially decrease the maximum rate of photosynthesis if these timings were  
12 synchronized, suggesting suboptimal canopy development (Zhao et al., 2022). The availability of  
13 nutrients varies little temporally, so its effect mostly accounts for the phenological variations in  
14 space rather than time.

#### 15 **4. Future directions**

16 Much work has been done in the field of land surface phenology, but the comparison between  
17 phenologies based on photosynthesis and canopy greenness warrant further study. We propose  
18 multiple directions of further exploration.

##### 19 *Understanding the relationship between SIF and VIs*

20 SIF has been suggested to be a robust proxy of photosynthesis in plants. This relationship, however,  
21 may decay under specific conditions, which can further affect the photosynthetic phenology  
22 retrieved using SIF. For example, the reduction in fluorescence and photochemical efficiencies  
23 during short periods of water stress do not have the same magnitude (van der Tol et al., 2014). Some  
24 studies have also reported limited changes in fluorescence efficiency, albeit with an evident  
25 decrease in photosynthesis (Helm et al., 2020; Marrs et al., 2020). No consensus, however, has been  
26 reached on how much uncertainty these limited changes would cause to the SIF-GPP relationship  
27 at the seasonal timescale (Y. Zhang et al., 2023). Recent studies have also suggested the importance  
28 of canopy structure and sun-sensor geometry in affecting the relationship between SIF and  
29 photosynthesis (Hao et al., 2021; Z. Zhang et al., 2018; Zhang and Zhang, 2023). SIF data are  
30 obtained at a nearly fixed time of the day by most sun-synchronous satellites, so the relationship  
31 between instantaneous SIF and daily photosynthetic carbon gain is also affected by light saturation,  
32 daily corrections of the level of solar radiation, and other factors. (Cheng et al., 2022; Y. Zhang et  
33 al., 2018b). Similarly, VIs have long been considered as proxies of canopy structure, and some  
34 studies have also used VIs to represent foliar area. Such approximations may have the problem of  
35 saturation, which could affect the calculation of peak timing. The seasonal variation of  
36 photosynthetic pigments and the accumulation of starch in leaves will change leaf reflectance,  
37 suggesting that the relationship between greenness and foliar area may change over time. A more  
38 accurate retrieval of photosynthetic and greenness phenologies warrant further analyses.

39 The differences between remotely sensed SIF and VIs can be quantitatively analyzed based on  
40 radiative transfer equations (Yang and van der Tol, 2018; Zeng et al., 2019). It is critical to identify  
41 the drivers of the differences between SIF and VIs at various timescales. How can we interpret the  
42 differences of phenology retrieved from these metrics, and under what circumstances do they  
43 represent or misrepresent the differences between photosynthetic and greenness phenologies?  
44 Answering these questions remain challenging due to limitations in both data and methods. Most  
45 SIF data sets are currently at coarse spatial resolutions and only cover a limited period, and the  
46 decomposition of SIF signals using radiative transfer equations relies on multiple assumptions that



1 may be invalid under specific circumstances. Harmonizing SIF data sets by combining multiple  
2 satellite observations may provide new opportunities for addressing these issues.

### 3 ***Effect of climate change on photosynthetic and greenness phenologies***

4 Climate change, especially global warming, has led to the widespread advance of spring phenology  
5 and a less-pronounced delay in autumnal phenology in the Northern Hemisphere. The effect on  
6 photosynthetic phenology, however, has been less clear. As discussed in the previous sections,  
7 multiple environmental factors could independently affect photosynthesis. It should be noted that  
8 the most influential factors may not be those that have the strongest trend. Some variables that do  
9 not have a clear trend with global warming may also play an important role in regulating  
10 photosynthetic phenology. A good example is solar radiation, whose effect on photosynthetic  
11 phenology may change with changes to the seasonality of vegetation canopy and other  
12 environmental factors (Zhang et al., 2020a).

13  
14  
15 Another important, but less explored, factor is the concentration of atmospheric CO<sub>2</sub>. Increased  
16 concentrations of atmospheric CO<sub>2</sub> may advance the onset of the growing season in spring and  
17 delay canopy senescence in autumn (Reyes-Fox et al., 2014), but it has a more direct effect on  
18 photosynthesis by increasing carboxylation (Walker et al., 2020). This effect of CO<sub>2</sub> fertilization is  
19 also temperature dependent and can affect the rate and peak timing of foliar development. The  
20 indirect effect of water saving effect may also alleviate water stress during the late growing season.  
21 The combined effect of CO<sub>2</sub> on photosynthetic phenology is less clear. A recent study using cities  
22 as natural laboratories suggested that urban heat islands and higher CO<sub>2</sub> concentrations may  
23 together extend photosynthetic phenology, but their respective contributions remain uncertain  
24 (Wang et al., 2019). It is still a challenge to solve this issue using remote sensing-based observations  
25 alone.

### 26 27 ***Combining photosynthetic and greenness phenologies to better understand the terrestrial carbon 28 cycle***

29 Photosynthetic and greenness phenologies provide important information on the physiological,  
30 structural, and functional dynamics of terrestrial ecosystems, which can help us to better understand  
31 the terrestrial carbon cycle. For example, how does altered foliar development affect ecosystem  
32 primary production? What drives the allocation of carbon to the foliage? Although previous studies  
33 have indicated that temperature and water stress may affect the fraction of carbon allocated to leaves  
34 and roots (Poorter et al., 2012; Reich et al., 2014), the temporal dynamics of such allocation, which  
35 directly affects greenness phenology, remain unclear.

36  
37 Together with other climate, eddy covariance, and atmospheric CO<sub>2</sub> observations, as well as  
38 aboveground biomass observations from microwave remote sensing, more research questions may  
39 be answered (Dannenbergh et al., 2020). For example, how do changes in photosynthetic and  
40 greenness phenologies affect the terrestrial carbon sink? Does water play an increasingly important  
41 role in regulating the uptake of terrestrial carbon late in the growing season? Satellite-derived  
42 photosynthetic and greenness phenologies can complement site-level observations and will provide  
43 important evidence for such large-scale analyses and model improvements.

## 44 45 **5. Concluding remarks**

46  
47 In this perspective, we provide an overview of recent progress in vegetation phenological research  
48 using both satellite-retrieved SIF and vegetation indices. The emerging satellite-retrieved and other  
49 reconstructed SIF data sets provide new opportunities for understanding the phenological responses  
50 of plants to climate change. We propose that the phenological metrics derived from these satellite

1 indicators should be understood from the perspectives of ecology, physiology, and remote sensing.  
2 New research opportunities should focus on the relationships between SIF and VIs, the impact of  
3 climate change on both photosynthetic and greenness-based land surface phenologies, and their  
4 impact on terrestrial carbon cycle.

#### 7 **Data availability**

8 The data used to generate Figure 2 are openly available from NASA  
9 (<https://e4ftl01.cr.usgs.gov/MOLT/MOD13C2.006/>) and the Qinghai-Tibet Data Center  
10 (<https://cstr.cn/18406.11.Ecolo.tpd.c.271751>)

#### 12 **Conflict of Interest**

13 The authors declare no conflict of interests.

#### 15 **Author Contributions**

16 Y. Zhang and J. Peñuelas designed and wrote the paper.

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