




## LETTER

# Climate change increases carbon allocation to leaves in early leaf green-up

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## Abstract

Global greening, characterized by an increase in leaf area index (LAI), implies an increase in foliar carbon (C). Whether this increase in foliar C under climate change is due to higher photosynthesis or to higher allocation of C to leaves remains unknown. Here, we explored the trends in foliar C accumulation and allocation during leaf green-up from 2000 to 2017 using satellite-derived LAI and solar-induced chlorophyll fluorescence (SIF) across the Northern Hemisphere. The accumulation of foliar C accelerated in the early green-up period due to both increased photosynthesis and higher foliar C allocation driven by climate change. In the late stage of green-up, however, we detected decreasing trends in foliar C accumulation and foliar C allocation. Such stage-dependent trends in the accumulation and allocation of foliar C are not represented in current terrestrial biosphere models. Our results highlight that a better representation of C allocation should be incorporated into models.

## KEYWORDS

allocation ratio, foliar carbon allocation, northern ecosystem, optimal partitioning theory, terrestrial biosphere models

Fandong Meng and Songbai Hong contributed equally.

## INTRODUCTION

Plant photosynthesis and respiration represent two key carbon (C) fluxes exchanged between the atmosphere and the biosphere. As atmospheric carbon dioxide (CO<sub>2</sub>) is uptaken into the biosphere through photosynthesis, the assimilated C is allocated to different plant organs (e.g. leaf, trunk, root) (Brüggemann et al., 2011; Chapin et al., 2002; Lambers et al., 1998) for varied functions (e.g. photosynthetic C fixation, height growth and water and nutrient uptakes; Brüggemann et al., 2011; Hartmann et al., 2020). However, while many studies have investigated the assimilation of C and plant respiration (Bond-Lamberty et al., 2018; Janssens et al., 2001; Keenan et al., 2013; Wehr et al., 2016), the research on C allocation has received much less attention in the field of ecosystem C cycling. Importantly, as plants are often subjected to different resource limitations and stress factors and have different inherited life-history strategies, the portfolios of C investment can change with shifts of dominant factors of resource limitations or stresses (Chen et al., 2020; Iwasa & Roughgarden, 1984; Reich et al., 2014). For example, more C could be allocated to nonphotosynthetic parts such as stems for harvesting light or to roots for absorbing belowground resources, depending on the main type of resource limitation (Guillemot et al., 2017; Litton et al., 2007; Poorter et al., 2012).

The modifications of C allocation with environmental changes are important for both plant autoecological growth and ecosystem C cycles (Friedlingstein et al., 1999; Konôpka et al., 2020; Vicca et al., 2012). Most studies on plant C allocation, however, have been conducted at the autoecological level, with few at ecosystem or regional scales. Factors of global change, particularly the increase in CO<sub>2</sub> concentration, extreme droughts and increasing nitrogen (N) deposition, may profoundly alter stress factors and the broad-scale availability of plant resources (Finzi et al., 2007; Kicklighter et al., 2019; Sardans et al., 2008). Therefore, a better understanding of large-scale variations in the strategies of plant C allocation in response to global change is essential for predicting vegetation dynamics and C cycles.

Recent advances in remote-sensing technology and data collection provide a potentially practical approach to investigate variations in the allocation of C between photosynthetic (leaves) and nonphotosynthetic (e.g. roots and stems) organs, both between years and within a growing season. In particular, deciduous plants grow leaves during the early part of growing season, but allocate more C to nonphotosynthetic organs at the peak of the season (Chapin, 1991; Pantin et al., 2012; Tilman, 2020). The exact allocation ratio between leaves and nonphotosynthetic organs during different stages of a growing season is difficult to obtain at broad scales, but remote sensing-based changes in the leaf area index (LAI) across these stages can be indicative of the amount of C allocated to leaves. Global greening identified using

LAI has been widely observed under anthropogenic climate change (Chen et al., 2019; Piao et al., 2020; Zhu et al., 2016), but it remains unknown how different stages of a growing season contribute to this greening trend and how the allocation of C across different stages is regulated by climate change.

Here, we used the increases in LAI ( $\Delta$ LAI) as a proxy for the allocation of C to leaves and explored the inter-annual trends in  $\Delta$ LAI in each month during the entire leaf green-up period in the Northern Hemisphere for 2000–2017 and further investigated how the trends were directly and indirectly regulated by environmental factors (e.g. temperature, soil-moisture content [SM] and solar radiation). Finally, we tested whether terrestrial biosphere models (TBMs) could identify the strategy used by plants to adapt to climate change by adjusting C allocation at different stages of leaf green-up period. Our work found that the accumulation of foliar C accelerated in the early green-up period and decreased in the late stage, but the TBMs did not capture the decreased trend due to an inaccurate representation of the C allocation strategy.

## MATERIALS AND METHODS

### Phenological metrics

We defined the leaf green-up period as the time between the start of the growing season (SOS) and the peak of the growing season (POS). SOS, defined as the date when the 2-band Enhanced Vegetation Index (EVI2) value first exceeded 15% (Gray et al., 2019), which is the phenological product of MCD12Q2 V6, calculated using data from the Moderate-resolution Imaging Spectroradiometer (MODIS) (downloaded from <https://lpdaac.usgs.gov/products/mcd12q2v006/>), available at 500-m spatial resolutions for 2001–2018. POS was defined as the date when annual LAI derived from the MOD15A2H v006 product was highest (details about the product are described below). The multiyear average dates of these two phenological metrics were converted from day of year into month of year, and then, the duration of the ecosystem green-up period was calculated as the difference between POS and SOS.

### Satellite-observed LAI

We used the LAI product of MOD15A2H v006 (<https://lpdaac.usgs.gov/products/mod15a2hv006/>) (Myneni et al., 2015). This product is available at 500-m spatial and 8-days temporal resolutions for 2000–2017 (Yan et al., 2016). Monthly LAI was used to perform further analysis. We first assigned each 8-days LAI data set to the month with the longest temporal overlap to obtain an accurate monthly LAI. For example, the LAI

data set for 2 February was assigned to January due to only two out of 8 days in February. We then extracted the monthly maximum as the proxy of monthly LAI, a method that is commonly known as maximal value composite (MVC) and has been broadly used in assessing satellite-derived vegetation growth due to its ability to reduce contaminations by clouds or aerosols (Verger et al., 2011). Meanwhile, for robustness evaluation, we also used monthly mean values. Focusing on the monthly scale also allows us to compare satellite-derived results with the modelled ones that are usually at the monthly temporal resolution (<http://dgv.m.ceb.ac.uk/index.html>). Some types of vegetation lacking strong seasonal dynamics (e.g. evergreen forests and barren soils) were excluded based on the land-cover classification of MCD12C1 v006 (<https://lpdaac.usgs.gov/products/mcd12c1v006/>) (Friedl et al., 2010). We also excluded regions where the annual maximum LAI occurred outside the March to October window. Another LAI product, CGLS (or the European Geoland2 Version 2 [GEOV2]); data input source: SPOT/VGT & PROBA-V (<https://land.copernicus.eu/global/products/lai>), was used to further verify the robustness of the results based on MODIS LAI. The spatial and temporal resolutions of the LAI product of CGLS (or GEOV2) were 1-km and 10-days, respectively, available from 1999 to the present. We rescaled the two LAI products to a resolution of 0.5° to match the meteorological data sets.

## Model-simulated LAI

The project ‘Trends and drivers of the regional scale sources and sinks of carbon dioxide’ (TRENDY) V7 is a dynamic global vegetation model project that simulates a factorial set of the Dynamic Global Vegetation Model (DGVM) simulations (<http://dgv.m.ceb.ac.uk/index.html>), which was used to test how well state-of-the-art TBMs could reproduce satellite-observed changes in monthly foliar C accumulation and corresponding dominant drivers. We chose monthly composites of LAI of the third simulation (S3), including CO<sub>2</sub>, climate and land use from 2000 to 2017. We used five models with a spatial resolution of 0.5° (the same as that of the observed meteorological data sets and resampled LAI data): the Dynamic Land Ecosystem Model (DLEM), Lund-Postam-Jena General Ecosystem Simulator (LPJ-GUESS), Land surface Processes and eXchanges (LPX), Vegetation Integrative Simulator for Trace gases (VISIT) and the Vegetation Integrative Simulator for Trace gases (ISAM). The corresponding driving factors of these models are climatic forcing (the Climatic Research Unit [CRU] and the CRU Japanese 55-year Reanalysis [CRU-JRA55]), rising levels of atmospheric CO<sub>2</sub> from both ice core and atmospheric observations, and land-use change (LUH2 data sets).

## Meteorological data sets

The mean 2-m surface temperatures were acquired from CRU.TS4.04 at a spatial resolution of 0.5° and a monthly temporal resolution, which were interpolated from ground meteorological stations ([https://crudata.uea.ac.uk/cru/data/hrg/cru\\_ts\\_4.04/cruts.2004151855.v4.04/](https://crudata.uea.ac.uk/cru/data/hrg/cru_ts_4.04/cruts.2004151855.v4.04/)) (Harris et al., 2020). Data of vapour pressure deficit (VPD) were also downloaded from CRU (Harris et al., 2020), which has the same spatial and temporal resolution as CRU temperature data. Soil-moisture (SM) at a depth of 2–5 cm was acquired from the C3S dataset provided by European Centre for Medium-Range Weather Forecasts (ECMWF) v201812.0.0 at a spatial resolution of 0.25° and a monthly temporal resolution (<https://cds.climate.copernicus.eu/cdsapp#!/dataset/satellite-soil-moisture?tab=overview>). Data for solar radiation were acquired from CRU-JRA v2.0, which is a combination of CRU and a Japanese reanalysed data set (JRA) (<https://catalogue.ceda.ac.uk/uuid/7f785c0e80aa4df2b39d068ce7351bbb>), at a spatial resolution of 0.5° and 6-hourly temporal resolution (Harris et al., 2014; Kobayashi et al., 2015). The SM data set was resampled to a spatial resolution of 0.5°.

## Photosynthesis indicators

We used the synchronously simulated gross primary productivity (GPP) dataset from the five models described above to represent the photosynthetic activity. Solar-induced chlorophyll fluorescence (SIF), a probe of photosynthesis (Baker, 2008), was used as a proxy for GPP in the satellite-observed data analysis due to the lack of long-term observational GPP data at large scale. The data of the contiguous SIF (CSIF) dataset were trained by a neural networks method using SIF from Orbiting Carbon Observatory-2 (OCO-2) and MCD43C1 v6 reflectance as input variables (Zhang et al., 2018), which has a 4-days temporal and 0.05° spatial resolutions, available from 2000 to 2020 (<https://doi.org/10.17605/OSF.IO/8XQY6>). Therefore, it makes up for the coarse spatiotemporal resolution and high uncertainty in the current SIF data set (Zhang et al., 2018).

## Data analysis

We used the increase in LAI ( $\Delta\text{LAI}$ ) in each month and throughout the green-up period to indicate the net allocation of C to leaves (hereafter leaf C), which is the difference between gross leaf C allocation and leaf respiration.  $\Delta\text{LAI}$  during green-up period was defined as annual maximum LAI minus LAI in the month before SOS, and monthly  $\Delta\text{LAI}$  was calculated as (Figure S1):

$$\Delta\text{LAI} = \text{LAI}_t - \text{LAI}_{t-1} \quad (1)$$

Because foliar growth is irreversible during the green-up period (Pantin et al., 2012),  $\Delta\text{LAI}$  should always be positive during this period. We thus discarded pixels with  $\Delta\text{LAI}$ s  $< 0$  (0.07%–2.4%, Figure S2) from analysis.

Linear regression was used to identify the interannual trends in  $\Delta\text{LAI}$  throughout the entire study period (Figure S1, Equation 2):

$$(\Delta\text{LAI})_i = a_i * (\text{Time}) + b_i \quad (2)$$

where time is the number of years from 2000 to 2017 for pixel  $i$ ,  $a_i$  is the temporal trend in  $\Delta\text{LAI}$  for pixel  $i$ ,  $b_i$  is the intercept for pixel  $i$ . For pixels with positive trends in green-up period  $\Delta\text{LAI}$ , we further defined the month contributing the most to the increase in  $\Delta\text{LAI}$  (the month with the largest positive trends in monthly  $\Delta\text{LAI}$ ) during the green-up period as the dominant month (TDM). The time between SOS and TDM is shown in Figure 1g. We further examined the temporal autocorrelation of  $\Delta\text{LAI}$  and found that there was no evident temporal autocorrelation of  $\Delta\text{LAI}$  across different months (Figure S3).

Both climate and photosynthetic C assimilation rate (GPP) could affect variations in  $\Delta\text{LAI}$ . Here, we performed two sets of partial correlation analyses to determine each grid's dominant factor responsible for satellite-observed temporal variations in  $\Delta\text{LAI}$  for each month during the leaf green-up period. In the first set, only climate factors, that is temperature, SM and solar radiation, were included as independent variables. Note

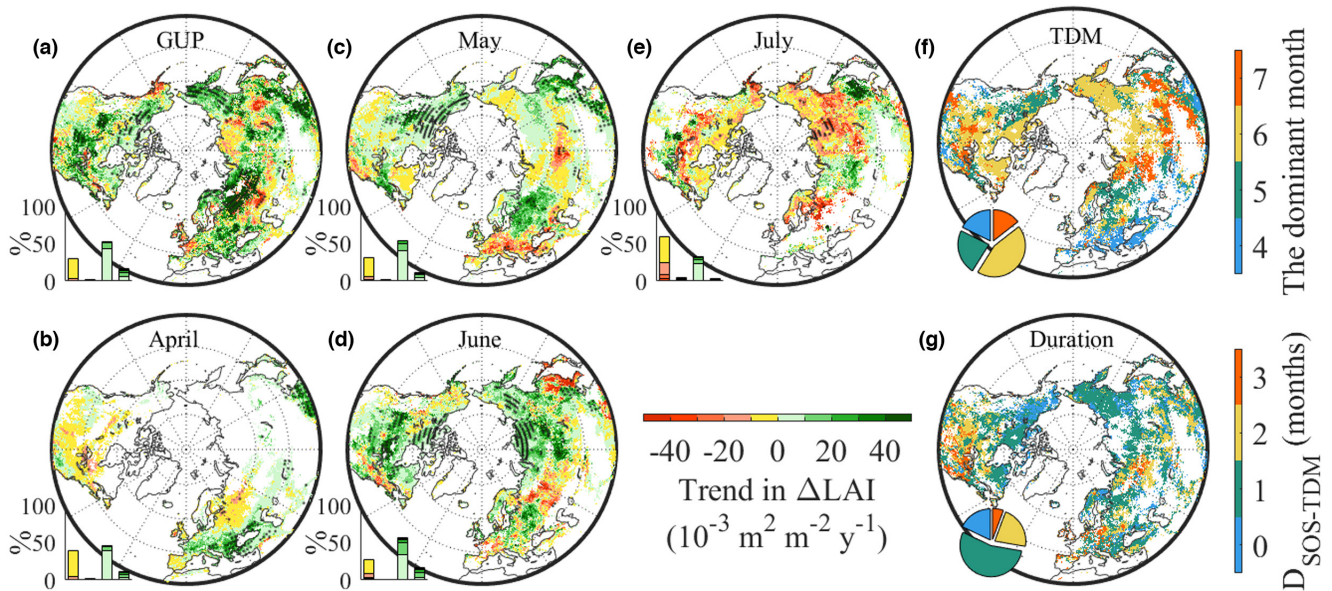
that the lagged effects of the climate factors were also considered by means of the pre-season period. The pre-season, defined as the period which most strongly affects phenological events (Menzel et al., 2006), was determined as the period preceding an event that exhibited the largest absolute value of partial correlation coefficient between  $\Delta\text{LAI}$  and a climate factor, after controlling for the other climatic factors.

In the second set of partial correlation analyses, we included both photosynthetic rate (using SIF as a proxy for observational data and GPP for modelled data) and climate factors. Furthermore, to examine the impact of atmospheric drought on  $\Delta\text{LAI}$ , we also conducted an additional partial correlation analysis between  $\Delta\text{LAI}$  and atmospheric VPD while controlling for other climate variables and SIF.

## RESULTS

### Changes in leaf C accumulation during the green-up period

The green-up period  $\Delta\text{LAI}$  (annual maximum LAI minus LAI in the month before the start of the growing season [SOS]) showed positive trends in most areas (71% of pixels) from 2000 to 2017 (Figure 1a). Monthly  $\Delta\text{LAI}$  (LAI in the current month minus LAI in the previous month), which is indicative of the intermonth



**FIGURE 1** Trends in  $\Delta\text{LAI}$  throughout leaf green-up period (GUP) and for each month of the GUP for 2000–2017. (a) Trends in  $\Delta\text{LAI}$  throughout GUP ( $\Delta\text{LAI}$  is defined as the difference between the annual maximum LAI and LAI in the month before the start of the growing season). They are parameters of  $a_i$  in Equation 2, same as subplots of (b–d). Trends in  $\Delta\text{LAI}$  for (b) April (monthly  $\Delta\text{LAI}$  is defined as the difference between LAI in the focused month and LAI in the preceding month), (c) May, (d) June and (e) July. Panels (a–e) share the same colour bar shown below (e). The black dots in (a–e) indicate significant trends at  $p < 0.05$ . The histograms in (a–e) are frequency distributions of the trend in  $\Delta\text{LAI}$ , the sequences of four bars represent the percentages of pixels with nonsignificantly negative trends, significantly negative trends, nonsignificantly positive trends and significantly positive trends, respectively. (f) The dominant month (TDM) contributing the most to the positive  $\Delta\text{LAI}$  trend in a. (g) Durations between SOS and TDM ( $D_{\text{SOS-TDM}}$ ). Only pixels with positive trends in (a) are shown in (f) and (g). The pie charts in (f) and (g) indicate the proportions of each group.

rate of foliar C accumulation, however, had divergent trends across different months (Figure 1b–e). For example, the trends in  $\Delta$ LAI in Europe were widely positive in April (Figure 1b) but negative in May (Figure 1c).  $\Delta$ LAI had widespread uptrends in North America in May (Figure 1c) and June (Figure 1d), but widespread uptrends in Siberia only in June (Figure 1d). This spatiotemporal heterogeneity of  $\Delta$ LAI trends is associated with vegetation phenology: earlier phenology coincided with the earlier occurrence of positive  $\Delta$ LAI trends, and vice versa. Indeed, if we defined the month contributing the most to the uptrend in  $\Delta$ LAI in green-up period as the dominant month (TDM) (Figure 1f), the duration from SOS to TDM was no more than 1 month in most areas (Figure 1g). Surprisingly, 78% of all pixels in July showed negative trends in  $\Delta$ LAI during 2000–2017 (Figure 1e), despite the widespread increase in July LAI over the same period (Figure S4d).

We also tested the robustness of the above results obtained with the Moderate-resolution Imaging Spectroradiometer (MODIS) LAI product (MOD15A2H v006) using monthly mean (instead of maximal) value as a proxy of monthly LAI (Figure S5), as well as using the Copernicus Global Land Service (CGLS) LAI product (data input source: the ‘Satellite Pour l’Observation de la Terre’ (SPOT) VEGETATION [SPOT/VGT] & the Project for On-Board Autonomy–Vegetation [PROBA-V]). The results consistently indicated that foliar C accumulation generally had positive trends in the early stage of green-up but negative trends in the late stages (Figure S6).

## Factors dominating leaf C allocation

We further performed partial correlation analyses between  $\Delta$ LAI and climatic factors (temperature, SM and radiation) to understand how changes in climatic variables may contribute to the observed trends in foliar C allocation during each month of the green-up period (Figure 2a–h). Since the climate of the preceding months (preseason) can also influence phenological dates and affect the rate of foliar C accumulation, we also included potential lagged effects of the climatic variables on  $\Delta$ LAI in additional analyses (Figure S7). The results suggested that temperature was the dominant climatic driver for  $\Delta$ LAI in the early green-up stage (Figure 2). For example, temperature in regions with the earliest onset of spring phenology (such as Europe and central and eastern North America, Figure S8) was often the dominant climatic factor positively associated with  $\Delta$ LAI in April, the month of spring onset, after controlling for SM and solar radiation (Figure 2a; Figure S9a). This dominant and positive effect of temperature on  $\Delta$ LAI extended to higher latitudes in May, including Canada and Siberia (Figure 2b; Figure S9b), but was not observed in the northernmost regions until June (Figure 2c; Figure S9c).

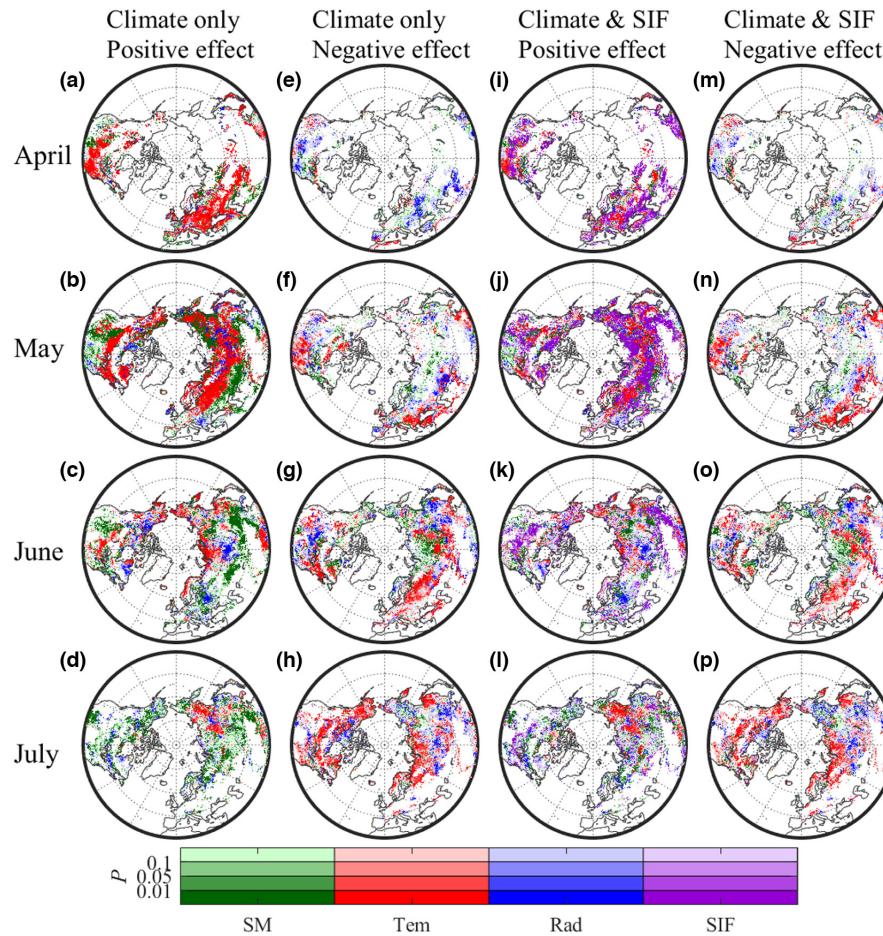
SM played a key role in regulating  $\Delta$ LAI in May for regions with continental climates such as inland Eurasia and North America (Figure 2b; Figure S9f), especially where the dominant type of vegetation is temperate and semi-arid grassland (Figure S10). For these regions, both SM and temperature jointly regulated foliar C accumulation in June, but with opposite effects on  $\Delta$ LAI (Figure 2; Figure S9). Across the whole study area, SM positively affected  $\Delta$ LAI in 56% of the pixels (Figure S9g), and temperature was generally negatively correlated with  $\Delta$ LAI (Figure S9c). These contrasting effects of SM and temperature on  $\Delta$ LAI were even more widespread in July, when  $\Delta$ LAI and SM were positively correlated in 65% of the pixels (Figure S9h).  $\Delta$ LAI and temperature were negatively correlated in 66% of the pixels (Figure S9d).

Interestingly, SIF was more strongly correlated with  $\Delta$ LAI than climatic variables in the early green-up stage (Figure 2). Temperature had a weakened, but still positive, effect on  $\Delta$ LAI after controlling for SIF (Figures S11–S13). In the late stage of the green-up period (May at low latitudes and June and July at higher latitudes), the correlation between  $\Delta$ LAI and SIF was generally weaker and even nonsignificant in most areas (Figure 2; Figure S11). The correlation between  $\Delta$ LAI and temperature in this late green-up stage did not change when SIF was or was not controlled for (Figures S11–S13).

## Assessing the performance of TBMs in C allocation simulations

The partial correlation analysis between modelled  $\Delta$ LAI and climatic factors (temperature, SM and radiation) with a potential lagged effect (Figure S14) indicated that the models could generally reproduce the apparent response of foliar C accumulation to climate change (Figure 3a–d; Figure 3e–l; Figure S15). Nonetheless, the partial correlations between modelled  $\Delta$ LAI and temperature in the late green-up stage were more negative than the satellite-based results (comparing Figures S15 and S9), suggesting a potentially overestimated apparent sensitivity of  $\Delta$ LAI to temperature by the models. These models also underestimated the apparent influence of SM on foliar C accumulation (Figure S15), especially in temperate and semi-arid grasslands, where satellite data indicated strong correlations between  $\Delta$ LAI and SM (Figure S9).

We also assessed whether the models could reproduce the climatic regulation of total assimilated C ( $C_{\text{total}}$ ) and leaf carbon allocation ( $P_{\text{leaf}}$ ) by including modelled gross primary productivity (GPP) as an independent variable in the partial correlation analyses (Figure 3m–t; Figure S16). The results suggested that the models generally replicated the weak effects of solar radiation on  $P_{\text{leaf}}$  and consequently on foliar C accumulation (Figure S17). However, models did not adequately simulate temperature and SM impacts on foliar C allocation (i.e.  $P_{\text{leaf}}$ ) (Figure 3m–t; Figure S16).



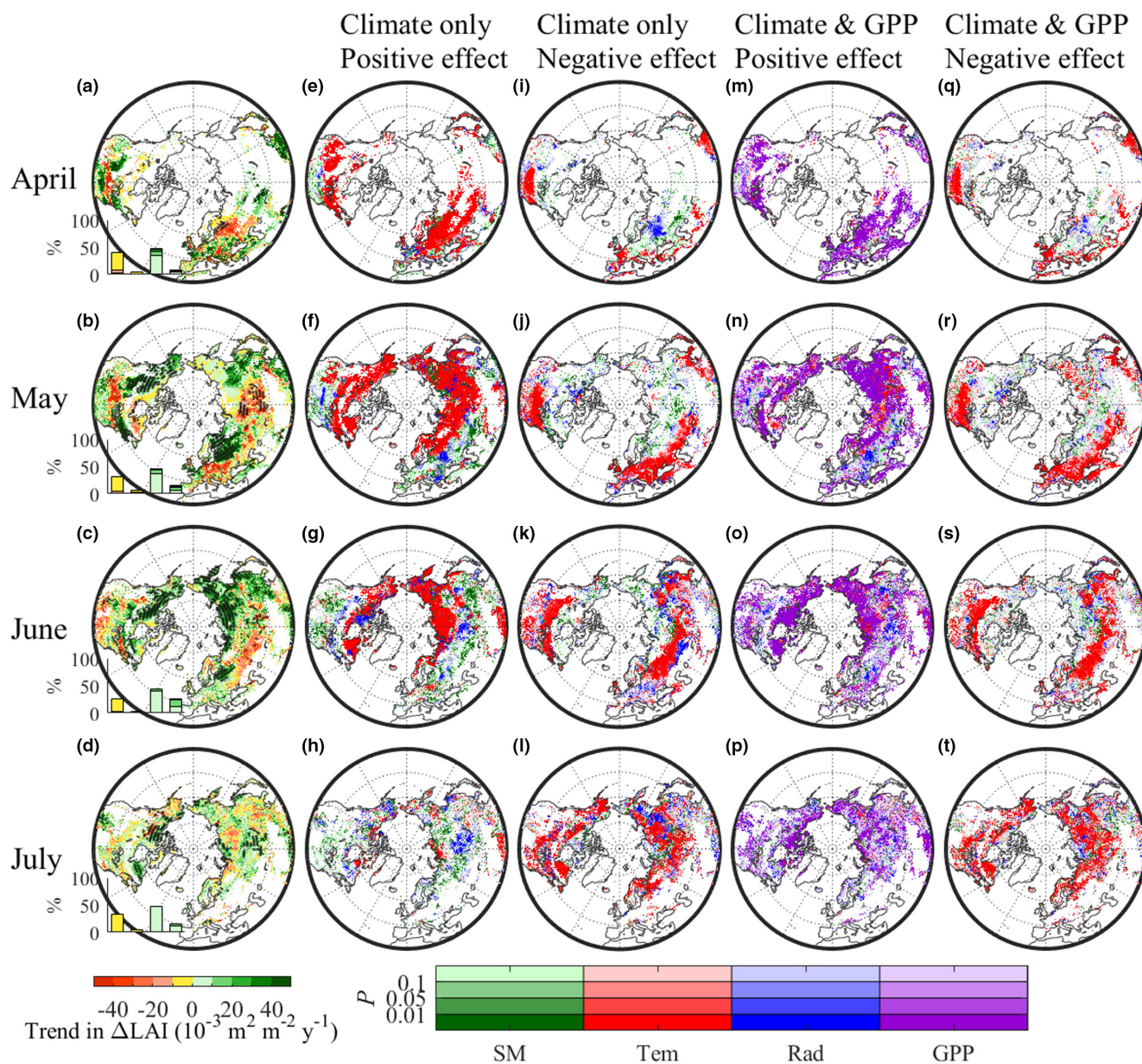
**FIGURE 2** Factors dominating the  $\Delta\text{LAI}$  trends for each month during leaf green-up period. The dominant factor is defined as the variable with the highest partial correlation coefficient after controlling for the other variables. Only climatic variables (soil-moisture content [SM], temperature [Tem] and solar radiation [Rad]) are considered in (a–h), and the three climatic variables and solar-induced chlorophyll fluorescence (SIF) in the focused month are considered in (i–p). Dominant factors positively correlated with  $\Delta\text{LAI}$  are shown in (a–d) (climate only) and (i–h) (climate and SIF), while those negatively correlated with  $\Delta\text{LAI}$  are shown in (e–h) (climate only) and (m–p) (climate and SIF) from April to July. Four intervals of  $|R|$  in [0 0.43], (0.43 0.50], (0.50 0.62] and (0.62 1] for (a–h) and in [0 0.44], (0.44 0.51], (0.51 0.64] and (0.64 1] for (i–p) correspond to  $p$ -values in (0.1 1], (0.05 0.1], (0.01 0.05] and [0 0.01], respectively. The pre-season length corresponding to the climatic data used for analysis is shown in Figure S3.

## DISCUSSION

Our study provides the first understanding on vegetation foliar C accumulation and allocation at large scales. We found that foliar C accumulation of the northern ecosystem is increasing during the early stage of green-up but decreasing in the late green-up stage over the past 18 years (2000–2017). Climate change can affect foliar C accumulation ( $C_{\text{leaf}}$ ) by impacting on total assimilated C ( $C_{\text{total}}$ ; Gampe et al., 2021; Wehr et al., 2016) and/or the proportion of C allocated to leaves ( $P_{\text{leaf}}$ ; Chen et al., 2020; Iwasa & Roughgarden, 1984; Reich et al., 2014) (Figure 4). In the early stage, we found that an increase in photosynthesis over the past 18 years was the primary factor contributing to the increase in foliar C accumulation, while temperature still contributed to the increase in  $C_{\text{leaf}}$  via affecting  $P_{\text{leaf}}$  even after accounting for its direct impact on  $C_{\text{total}}$ . This preference of plants to allocate more C to leaves in the early green-up stage under warming is likely

because vegetation productivity is more limited by the foliar surface than by the access of roots to soil water and nutrients (Chapin et al., 2002; Chen et al., 2020).

In the late stage, the increase in foliar photosynthesis did not necessarily increase the accumulation of foliar C. As canopies close in this stage, vegetation productivity is more constrained by the availability of water and nutrients than by the number of leaves for photosynthesis, resulting in more C invested in non-photosynthetic plant organs for acquiring resources (Chapin et al., 2002; Chen et al., 2020). A higher temperature during this late green-up stage generally increases plant autotrophic respiration (Chapin et al., 2002) more than it increases photosynthesis because of the rising respiratory cost at a temperature above the optimal level (Drake et al., 2016). Allocating more C to leaves under temperature increases in this late green-up stage is therefore not economical (Bloom et al., 1985; McCarthy & Enquist, 2007). Warming can

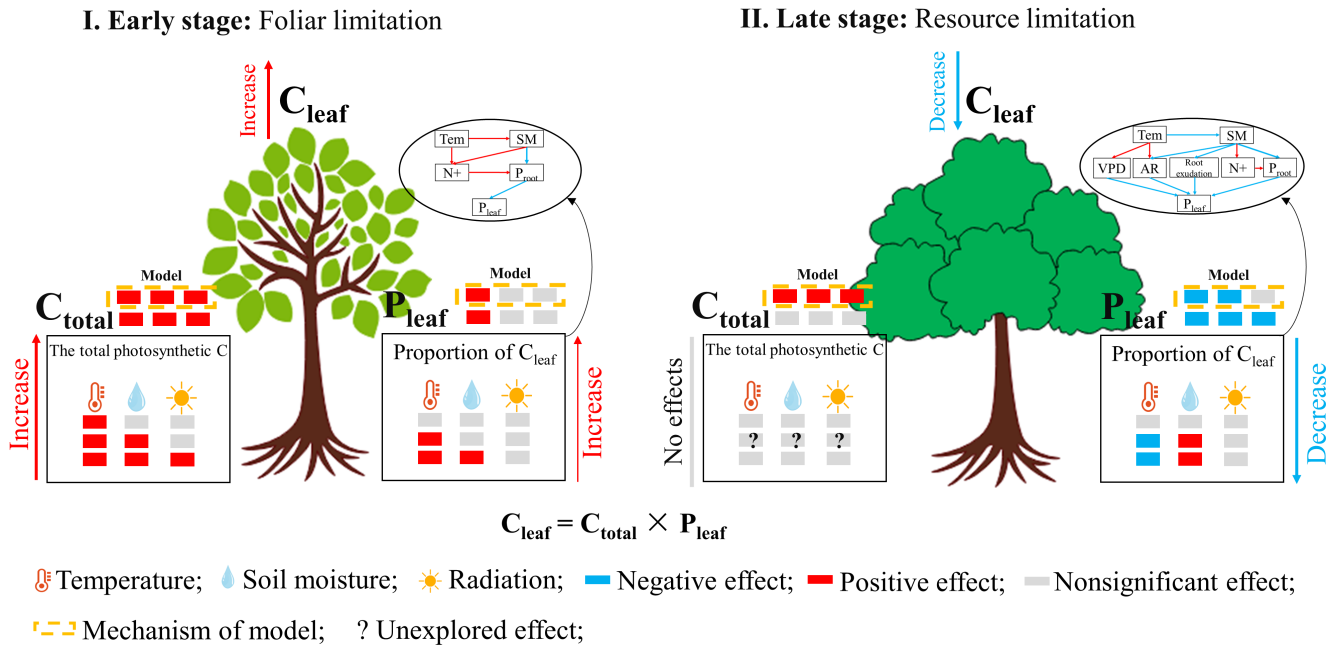


**FIGURE 3** Trends in modelled  $\Delta\text{LAI}$  and their dominant driving factors for each month during leaf green-up period. Trends in modelled  $\Delta\text{LAI}$  in (a) April (monthly  $\Delta\text{LAI}$  is defined as the difference between LAI in a month and that in the preceding month), (b) May, (c) June and (d) July for 2000–2007. Panels (a–d) share the same colour bar shown below (d). The black dots in (a–d) indicate significant trends at  $p < 0.05$ . The histograms in (a–d) are frequency distributions of the trend in  $\Delta\text{LAI}$ . (e–t) Factors dominating the modelled  $\Delta\text{LAI}$  trends for each month during leaf green-up period. The dominant factor is defined as the variable with the highest partial correlation coefficient after controlling for the other variables. Only climatic variables (soil-moisture content [SM], temperature [Tem] and solar radiation [Rad]) are considered in (e–l), and the three climatic variables and gross primary productivity (GPP) for the focused month are considered in (m–t). Dominant factors positively correlated with  $\Delta\text{LAI}$  are shown in (e–h) (climate only) and (m–p) (climate and GPP), and dominant factors negatively correlated with  $\Delta\text{LAI}$  are shown in (i–l) (climate only) and (q–t) (climate and GPP). Four intervals of  $|R|$  in [0 0.43], (0.43 0.50], (0.50 0.62] and (0.62 1] for (a–h) and in [0 0.44], (0.44 0.51], (0.51 0.64] and (0.64 1] for (i–p) correspond to  $p$ -values in (0.1 1], (0.05 0.1], (0.01 0.05] and [0 0.01] respectively. The preseason length corresponding to the climatic data used for analysis is shown in Figure S9.

also increase atmospheric VPDs and induce water stress (Yuan et al., 2019), which can become increasingly important in limiting vegetation productivity from the early to late green-up stages and thus diverting more C investment to organs for acquiring and transporting water (Guillemot et al., 2017; Hartmann et al., 2020). This indirect effect of temperature by increasing VPD

was particularly possible in Europe (Figure S18b) and North America (Figure S18d), where the significantly negative correlation between  $\Delta\text{LAI}$  and temperature was weakened and even disappeared when VPD was further controlled for.

Regarding the impacts of SM and solar radiation on foliar C accumulation during the green-up period, solar



**FIGURE 4** Schematic of the climatic regulation of foliar C accumulation. The allocation of C to leaves ( $C_{\text{leaf}}$ ) is determined by both the total amount of assimilated photosynthetic C ( $C_{\text{total}}$ ) and the proportion of C allocated to leaves ( $P_{\text{leaf}}$ ), that is  $C_{\text{leaf}} = C_{\text{total}} \times P_{\text{leaf}}$ . (I) The accelerating accumulation of foliar C in the early stage of green-up is attributed to increases in photosynthesis and  $P_{\text{leaf}}$ . (II) The negative trend in the accumulation of foliar C in the late stage is mainly due to a decrease in  $P_{\text{leaf}}$  driven by climate but is weakly linked with photosynthesis. Potential mechanisms by which climate regulates  $P_{\text{leaf}}$  are shown in the ovals, where red arrows indicate positive effects and blue arrows indicate negative effects. Models overestimate the link between photosynthesis and the allocation of C to leaves and skew the change in  $P_{\text{leaf}}$  under climate change, which leads to mismatches between the models and satellite observations for the  $\Delta\text{LAI}$  trend in the late stage of green-up period.

radiation noticeably affected  $C_{\text{leaf}}$  in May (Figure S9) by increasing photosynthetic  $C_{\text{total}}$  (Figures S9, S11). In contrast, SM could potentially affect  $C_{\text{leaf}}$  by affecting both  $C_{\text{total}}$  and  $P_{\text{leaf}}$  (Figures S9, S11), which is worth further studies. Increasing the availability of soil water can increase  $C_{\text{total}}$  (Liu et al., 2020; Reich et al., 2018), but little is known about how variations in SM may also lead to trade-offs in C allocation between leaves and other organs (Bloom et al., 1985; Tilman, 2020). Several mechanisms may have contributed to the observed impact of SM on  $P_{\text{leaf}}$  (Figure 4). First, high SM can relieve plant water stress and reduce the need for C investment for acquiring and transporting water (Guillemot et al., 2017; Litton et al., 2007; Poorter et al., 2012), which can shift more C to leaves and hence increase  $P_{\text{leaf}}$ . Second, an increase in SM can increase the activities of soil microbes and accelerate the mineralization of soil N and phosphorus (Finger et al., 2016; Keuper et al., 2012), which can also reduce the need of allocating more C to root systems (Guillemot et al., 2017; Litton et al., 2007; Poorter et al., 2012). Meanwhile, increasing N availability could stimulate plants to allocate more C to leaves for assimilating more C to maintain the C: N stoichiometric ratio. Third, when SM is low, a decrease in  $P_{\text{leaf}}$  saves water and reduces respiratory C loss (Metcalfé et al., 2010). Fourth, root exudation can also compete with leaves for C under drought, because thirsty tree roots exude more C (Heinemeyer et al., 2012; Preece et al., 2018).

Correct schemes for C allocation simulations are essential for the accurate prediction of vegetation dynamics and ecosystem C cycles by process-based TBMs. However, TBMs could well capture the early stage of foliar C allocation but overestimate it in the late stage of green-up. Parallel analysis like observations, the overestimation of foliar C allocation during the late stage of green-up was caused by the neglect of the SM effect on foliar C accumulation. The inadequacy of TBMs in capturing apparent sensitivities of foliar C accumulation to these climatic variables is likely due to the following three reasons.

First, the models overestimated the link between photosynthesis and C allocation to leaves in the late stage of green-up (Figure 3; Figure S16), which may explain why the models could not reproduce the widespread downward trends in  $\Delta\text{LAI}$  during July (Figure 3d, 38% pixels for the models versus 78% pixels for the satellite-based results exhibiting negative trends in  $\Delta\text{LAI}$ , Figure 1e). Satellite-based findings indicated that the increase in foliar photosynthesis did not necessarily increase foliar C accumulation in the late stage of green-up. Four of the five models (all except LPX, Figure S19), however, generated strong positive correlations between GPP and  $\Delta\text{LAI}$  in this stage, which could lead to false-positive feedbacks that in turn lead to the overestimation of vegetation productivity. Second, three of the models (LPJ-GUESS, LPX and VISIT, Figure S20) replicated the negative effect of



temperature on foliar C accumulation by influencing  $P_{\text{leaf}}$  in the late stage of green-up but overestimated the strength of this negative effect. The other two models either produced a positive effect of temperature on  $P_{\text{leaf}}$  (and consequently on foliar C accumulation) in the late stage of green-up or a weak correlation between  $\Delta\text{LAI}$  and temperature throughout the green-up period, both in contrast to the satellite-derived results. These models may have skewed the trade-offs of C allocation between organs under changing temperatures. Third, surprisingly, none of the five models reproduced the positive effect of SM on  $P_{\text{leaf}}$  or  $\Delta\text{LAI}$  (Figure S21), which may be another reason for the mismatch between the models and satellite observations in the  $\Delta\text{LAI}$  trend in the late stage of green-up period. Optimizing the response of C allocation in TBMs to different drought stresses would likely improve their performance.

There are also uncertainties related to our approach of using LAI as a proxy of leaf C for temporal variation analyses. By definition, leaf biomass is the result of LAI divided by specific leaf area (the ratio of fresh leaf area to dry leaf biomass). Here, we assume SLA is invariant for a given grid over the interannual scale. While this assumption is reasonable when a given grid's vegetation type does not change from year to year, we are aware of potential uncertainties associated with this invariant SLA assumption. In particular, SLA may change with year-to-year climate variation, light exposure (sunlit vs. shaded; Chen et al., 2014) and forest age (Gao et al., 2022). Indeed, an experimental study showed a slight change in SLA over time due to opposite effects caused by temperature and  $\text{CO}_2$  (Tjoelker et al., 1999). However, there is no long-term and large-scale in situ measured dataset of SLA including the broadly used TRY database that allows us to explore long-term SLA changes over years. Future advances in observing networks of plant traits may help better incorporate SLA change in ecosystem leaf C allocation research.

In addition, our analyses were conducted at a spatial resolution of  $0.5^\circ \times 0.5^\circ$ , which is fairly coarse and may lead to considerable uncertainties. For example, for a mixed pixel especially in ecological transition zones, changes in LAI may have also been caused by vegetation type shift rather than by climate change which is the focus of this study. This coarse resolution may also mask fine-scale processes and mechanisms (Bradford et al., 2017; Levin, 1992) that could have been important for understanding ecosystem leaf C allocation responses to climate change. Hence, future studies need to test the phenomena and possible mechanisms revealed in this work at a finer scale.

In summary, we provided the first account of how foliar C accumulation and allocation changed during different stages of the green-up period from 2000 to 2017 at the landscape level using data sets of satellite-derived LAI and SIF. Our results highlight an accelerating accumulation of foliar C during the early stage of green-up

due to the increases in both total photosynthesis and the proportion of photosynthetic C allocated to leaves under recent climate change. In contrast, foliar C accumulation during the late green-up stage showed a decreasing trend. The divergent trends of foliar C accumulation in the early versus late stages of green-up are consistent with the optimal partitioning theory, which has been verified at the level of individual plants, but never at the broader landscape level before. This landscape-level optimized C allocation scheme between photosynthetic and nonphotosynthetic plant organs in response to climate changes has important implications for the global change modelling community. TBMs are currently inadequate for modelling the response of C allocations to climatic variations at different stages of vegetation growth, in particular the overestimation of foliar C allocation during the late stage of green-up and the neglect of the SM effect on foliar C accumulation. This lack of capacity in C allocation simulations may be one of the sources for the large uncertainties in modelling C cycle responses to climate change.

Reducing model uncertainties requires better parameterization and description of the C allocation scheme and its dynamics with vegetation seasonal cycles and climate change. Clearly, integrated studies combining data from manipulative field experiments and long-term observations of plant C allocation are valuable for model development and verifications. On the contrary, ecological theories of optimal resource acquisition provide critical guidelines in developing and refining climate change adapted allocation schemes used in TBMs, which can also be extended to other components (such as roots) where empirical experimental and observational data are even more difficult to obtain over broader scales. Furthermore, while direct evidence from in situ long-term biomass observations is lacking, our findings will inspire new research, especially that using networks of coordinated ground monitoring (e.g. the NEON system), to further test the hypothesis and improve our understanding of carbon allocation under climate change.

## AUTHOR CONTRIBUTIONS

Shilong Piao designed the research. Fandong Meng and Jiawei Wang performed analysis and created all figures. Songbai Hong, Fandong Meng, Anping Chen and Shilong Piao created the first draft of the paper. All authors contributed to the interpretation of the results and to the text.

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## CONFLICT OF INTEREST STATEMENT

There are no conflicts of interest to declare.

## PEER REVIEW

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## DATA AVAILABILITY STATEMENT

All data supporting the results are publicly available. Codes supporting the results are available in Figshare: <https://doi.org/10.6084/m9.figshare.21317637.v2>.

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