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Title: Plant phenology and global climate change: current progresses and challenges

Running head: Plant phenology and global climate change

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Abstract

Plant phenology, the annually recurring sequence of plant developmental stages, is important for plant functioning and ecosystem services and their biophysical and biogeochemical feedbacks to the climate system. Plant phenology depends on temperature, and the current rapid climate change has revived interest in understanding and modelling the responses of plant phenology to the warming trend and the consequences thereof for ecosystems. Here, we review recent progresses in plant phenology and its interactions with climate change. Focusing on the start (leaf unfolding) and end (leaf coloring) of plant growing seasons, we show that the recent rapid expansion in ground- and remote sensing- based phenology data acquisition has been highly beneficial and has supported major advances in plant phenology research. Studies using multiple data sources and methods generally agree on the trends of advanced leaf unfolding and delayed leaf coloring due to climate change, yet these trends appear to have decelerated or even reversed in recent years. Our understanding of the mechanisms underlying the plant phenology responses to climate warming is still limited. The interactions between multiple drivers complicates

the modelling and prediction of plant phenology changes. Furthermore, changes in plant phenology have important implications for ecosystem carbon cycles and ecosystem feedbacks to climate, yet the quantification of such impacts remains challenging. We suggest that future studies should primarily focus on using new observation tools to improve the understanding of tropical plant phenology, on improving process-based phenology modelling, and on the scaling of phenology from species to landscape-level.

1. Introduction

Phenology is the study of periodically recurring patterns of growth and development of plants and animal behavior during the year (Lieth, 1974). This subject has a long history that can be dated back to thousands of years ago when our ancestors realized that the documentation of some recurring phenological phenomena could be useful for the guidance of agricultural decisions. Over its long history, phenology has grown from an empirical subject of observing and recording the timing of a few key annual natural events for a handful of species to a comprehensive field that involves expanded observations, experiments, and modelling. This long history can be roughly divided into three major periods (Figure 1, Table S1). The first period (1300 B. C. E – around 17th century) was characterized with the identification of seasonal rhythms that are important for arranging agricultural activities. Phenology during this period was more like empirical descriptions of naturally reappearing phenomena of plants and animals. The second period (17th century – 1990s) marked the birth of phenology

as a scientific subject and its initial growth. During this period, geographers and natural historians started to record the timing of various phenological events and to investigate mechanisms behind them with statistical and experimental approaches. Reaumur first introduced the concept of "degree-day" in 1735 (Reaumur, 1735) and Charles Morren coined the word "phenology" in 1853. Statistical models between the timing of phenological events and climatic factors were developed (Schwartz, 2013), and new experiments were conducted to understand mechanisms underlying observed phenological patterns and variations. Also, during this period, phenology observation networks started to be set up across the globe (Barck *et al.,* 1753; Defila, 2008; Chen, 2013). The third and current period is the modern phenology era (1990s to the present), during which the rapid development of more sophisticated monitoring techniques and modelling approaches has greatly stimulated the rapid progress of phenology studies. With the increased concern of global climate change and its potential impacts, the establishment of international phenology networks has facilitated collective efforts on large-scale and standardized phenological data collection and sharing (Chmielewski F.M *et al.*, 2013; Templ *et al.*, 2018). Meanwhile, rapid progresses in remote sensing technologies have greatly expanded the scope of phenology studies (White *et al.*, 1997; Zhang *et al.*, 2003), dramatically improving our understanding of vegetation phenology from local to the globe. There is no question that the broad use of satellite data has stimulated the emergence of macro-scale phenology in the era of global change. Similarly, manipulative experiments have provided new insights into mechanistic understanding of phenological processes

(Cleland *et al.*, 2007); and new process-based models have largely enhanced our ability in predicting phenological changes under varied climatic and anthropogenic scenarios (Jeong *et al.,* 2013a; Chuine & Régnière, 2017).

The fast growth of phenology research over recent decades has provided critical information on how ecosystems may respond to climate change. Recent climate change has greatly shifted the timing of major phenological events, like the widely reported spring advancement and autumn postponement (Menzel *et al.*, 2006; Piao *et al.*, 2006; Jeong *et al.*, 2011; Gill *et al.*, 2015); and has caused phenological mismatches across trophic levels (Tylianakis *et al.*, 2008; Renner & Zohner, 2018). Such significant phenology changes under climate change can have strong impacts on community structures and ecosystem functions (Suttle *et al.*, 2007; Yang & Rudolf, 2010). For example, the different phenological responses to warming between plants and animals may result in bird species not breeding at the time of maximal food supply (Merila *et al.*, 2001; Matthysen *et al.*, 2011) or cause the reduction in seed production for some tree species (Kudo & Ida, 2013). Warming induced changes in phenology is also a primary cause for the recent increase in vegetation activity and carbon uptake (Piao *et al.*, 2017). Changes in plant phenology may also feedback to the climate system through its role in modifying water and energy exchanges between terrestrial ecosystems and the atmosphere (Peñuelas & Filella, 2009; Richardson *et al.*, 2013). Hence, improved knowledge of phenology changes, their

key drivers, and ecosystem impacts is essential for better understanding and modelling the interactions between ecosystems and the climate system.

With the recent rapid advancement of phenology studies and the establishment of their crucial role in global change science, it is important to critically review recent progresses in this field, to provide important insights in how to advance knowledge, to optimize future studies and to make phenology a predictive science. Therefore, here we conduct a systematic and critical review synthesizing current research progresses in plant phenology. We focus this review on plant phenology as plants are primary ecosystem producers. More specifically, we limit our review to the start (leaf unfolding) and end (leaf coloring) dates of plant growing seasons. These dates are sensitive to climate change, determine the length of the growing season, and have significant ecosystem carbon cycle and climate implications. In the following sections, we will first summarize current methodological progresses. Then we will identify key findings of current climate change-induced plant phenological changes, based on ground and satellite observations, and review their major drivers and mechanisms. Furthermore, given the increasing concern of climate change and the strong linkage between plant phenology and climate, we will recap current understanding on the ecological consequences and climate feedbacks of observed plant phenological changes. Finally, we will discuss the main challenges in future plant phenology studies.

2. Methodological Advances in Plant Phenology Research

2.1 Ground-based phenology observations

Ground-based observation is a traditional (Sparks & Carey, 1995; Aono & Kazui, 2008), but still highly useful method in phenology studies and provides first-hand direct evidence of phenological changes. Ground-based observations can accurately record the timing of phenological events for specific sites and species. Networks of long-term ground-based phenology observations are particularly useful to investigate phenological variations across a broad geographical range and its possible changes in response to climate change (Cleland *et al.*, 2007). Recently, with the development of smartphone and wireless communication technology, citizen science elevates ground-based phenology observations to a new height and greatly expands the recording of phenological events over a large area and for many more species (Dickinson *et al.*, 2012; Hufkens *et al.*, 2019).

While ground-based phenology observation is valuable for climate change studies, this method is also subject to some shortcomings. First, the spatial distribution of ground phenology observations is highly uneven. Observations are largely concentrated in temperate and subalpine forests, and very scarce in grasslands and in subtropical and tropical areas. Unclear seasonal variations in these regions adds to the difficulty of detecting their phenological changes (Schwartz, 2013). Ground-based observations are also rare in harsh environments, such as arctic and alpine tundra ecosystems, or in arid desert ecosystems (Richardson *et al.*, 2013). Second,

ground-based observations often involve different observers and methods. Without uniform protocols to describe phenological events, it is difficult for data interchange and integration among different regions or researchers. The well-known BBCH (Biologische Bundesanstalt, Bundessortenamt und CHemische Industrie) system is a good example that has provided a uniform definition of plant development stages (Meier *et al.*, 2009). Nonetheless, even with the BBCH system, it is still difficult to coordinate all ground-based observations with the same criterion, because varied definitions for individual stages are adopted among different researchers. Third, while citizen scientists greatly expand the extent and volume of phenology observation data, their quality is often doubtful (Mayer, 2010) and it remains a grand challenge to and conduct systematic big data analyses and extract phenological patterns from these data with variable quality.

2.2 Remote-sensing-based phenology observations

During the past few decades, the emergence of remote sensing techniques has greatly expanded the horizon of traditional plant phenology observations. In particular, data from satellite remote sensing have been widely applied in the study of landscape-scale plant phenology by detecting the timing of phenological events in the temporal profile of greenness-related vegetation indices, such as the normalized difference vegetation index (NDVI) and the enhanced vegetation index (EVI) (Zhang *et al.*, 2003; Piao *et al.*, 2006; Liu *et al.*, 2018b). Taking NDVI- or EVI-derived phenology as an example, the translation from satellite data to phenological events

usually includes the following three steps: 1) improving the quality of NDVI or EVI datasets, 2) fitting one or multiple functions to the seasonal NDVI or EVI patterns, and 3) identifying the start and end dates of the growing season using either predetermined thresholds or inflection points (White *et al.*, 2009; Liu *et al.*, 2016a). However, multiple factors can contribute to reduced accuracy of satellite-derived estimates of plant phenological events, such as poor observation conditions (e.g. clouds, snow and ice), BRDF (bidirectional reflectance distribution function) effects, shifts in sensors (Tucker *et al.*, 2005; Pinzon & Tucker, 2014), and coarse spatial and temporal resolutions. For example, the coarse spatial resolution of satellite data (ranging from 30 meters to several kilometers) can make the retrieval and interpretation of phenological dates particularly challenging in mixed canopies where a mixture of species in different phenological phases co-occur at the same time (White et al., 2009). Similarly, in deciduous forests, greening often occurs first at the ground level, implying that the spring greening date as identified by remote sensing approaches may reflect the greening date of herbs and shrubs, and not that of the dominant trees in these forests that tend to green-up later (Fu *et al.*, 2014b).

In addition, it is a common practice to retrieve plant phenology from seasonal changes in satellite greenness indices, which change little for evergreen vegetation such as tropical and boreal evergreen forests. Recently, remotely sensed solar-induced chlorophyll fluorescence (SIF) data have emerged as useful tools to study seasonal variations in gross primary productivity (GPP) (Meroni *et al.*, 2009;

Smith *et al.*, 2018). Due to its direct link to photosynthetic activity and its insensitivity to cloud and atmospheric scattering, SIF also provides an alternative approach in retrieving phenology events for evergreen subtropical and tropical forests (Joiner *et al.*, 2014; Bertani *et al.*, 2017). However, the temporal and spatial resolution of the currently available satellite derived SIF data is still very coarse (Jeong *et al.*, 2017; Sun *et al.*, 2017), and needs to be improved in future missions to enable better representation of phenological events using SIF.

In addition to satellite-induced vegetation greenness indices and SIF, near surface remote sensing has also boomed in the past decade and can be useful for phenology studies due to its repeated, high frequency image collection (every half to one hour) using commercial networked cameras. These camera-based phenology observation networks have been established in the US, Japan, and Europe (Nasahara & Nagai, 2015; Peichl *et al.*, 2015; Richardson *et al.*, 2018a), and are under construction in China. Most of these cameras are located in carbon flux measurement sites for retrieving plant phenology data at landscape or species levels (Tang *et al.*, 2016). It is noteworthy that these phenology cameras need to be calibrated against a spectroradiometer prior to being implemented at field sites. When using *in situ* phenology cameras, observing geometries, including zenith and azimuth angles, and the sensor field of view need to be constant among sites. Obtained photos also need to be calibrated to minimize BRDF effects and changes in incident radiation. Most photos from phenology cameras only provide digital number (DN) values rather than

reflectance, and the interpretation of phenological events from those DN values requires more caution during image processing (Wingate *et al.*, 2015). The above limitations of phenology cameras could be potentially overcome by using unmanned aerial vehicles (UAV) with spectroradiometer onboard, which can provide multispectral or hyperspectral images varying from the plant level to the landscape scale and thus establish a direct spatial linkage between field- and satellite- based observations (Klosterman *et al.*, 2018). When automated, the temporal resolution of UAV sensing can be maximized during spring and autumn for improved accuracy of plant phenology monitoring.

2.3 Multi-source data fusion

Data accumulation through remote sensing-based phenology observations has greatly enhanced our capacity in detecting phenological events and understanding their association with climate and other environmental factors over a broad geographical range. Nonetheless, as already hinted to above, data acquisition via remote sensing also has its own handicaps. For example, recent studies suggested that the coarse resolution (from 250 m to 8 km) of satellite data leads to considerable biases in the detection of plant phenological events, particularly when the land surface is highly heterogeneous (Zhang *et al.*, 2017). The coarse resolution of satellite images can also cause inconsistency between results deduced from remote sensing and from *in situ* observations (Fu *et al.*, 2014b). The fusion of different spatiotemporal datasets can help mitigate these problems through generating

time-series data with both high spatial resolution and higher frequency. To date, there have been more than 60 spatiotemporal data fusion models developed using different principles and strategies (Zhu *et al.*, 2018). These fusion models can include un-mixing based, weight function based, Bayesian based, learning based models, and hybrid ones (Gao *et al.*, 2006; Zhu *et al.*, 2010). Among these models, the spatial and temporal adaptive reflectance fusion models (STARFM, Gao *et al.* (2006)) and the enhanced STARFM (ESTARFM, Zhu *et al.* (2010)) are the most popular ones for plant phenology monitoring because of their simplicity and robustness. Studies using fused satellite images have obtained satisfactory phenology estimates, since time series derived from fused images can well characterize plant seasonality and are highly correlated with field observations (Walker *et al.*, 2014).

With the increase of freely available satellite products, we can foresee that synthesized satellite images by data fusion will be even more widely used for plant phenology monitoring. In the future, we suggest that the following key perspectives in phenology data fusion can be particularly noteworthy: (1) fusing images from different types of sensors, (2) focusing on longer time series, (3) increasing robustness when fusing noisy data, and (4) generating publicly accessible datasets. The spatiotemporal data fusion techniques, combined with multi-scale phenological observations (Figure 2) will create unprecedented opportunities for validating satellite retrievals of plant phenology, especially for heterogeneous land surfaces.

2.4 Manipulative experiments of phenological responses to climate change

Ground- and remote sensing- based observations provide direct evidence of spatial variations in plant phenology and its eventual temporal trends and differences. However, plant phenology is responsive to multiple environmental factors, which themselves are often correlated (Keenan & Richardson, 2015; Richardson *et al.*, 2018b). Therefore, using only phenology observations it is extremely difficult to deconvolute the impacts of the different covarying drivers of phenology and to gain insight in the mechanisms underlying observed patterns in the observations and changes therein. In pursuing mechanistic understanding of plant phenology, manipulative experiments have been proven a very useful tool. Two broad types of climate warming experiments, i.e. passive and active warming, have been used in phenology studies (Aronson & McNulty, 2009). Results from both methods have generally reached similar conclusions, e.g. that spring leafing is highly sensitive to manipulative warming (Arft *et al.*, 1999; De Frenne *et al.*, 2010). While manipulative experiments have enriched our mechanistic understanding of phenological responses to climate change, these experiments also have some inherent shortcomings. First, most manipulative experiments are conducted for a handful of species and usually have only lasted for a few years. Such short-term warming experiments may not suffice to induce adaptive responses or to gain complete understanding of long-term phenological responses of plants to environmental changes (Wolkovich *et al.*, 2012). This is because other ecological processes, such as thermal acclimation and changing nutrient availability, may play a gradually increasing role over time, and

thereby alter the original short-term phenological responses (Leuzinger *et al.*, 2011). Second, these manipulative experiments are normally conducted on seedlings or saplings (Gunderson *et al.*, 2012; Primack *et al.*, 2015), but rarely on mature trees. However, young and mature trees may show substantially different phenological responses to the same environmental changes (Vitasse *et al.*, 2014). Ontogenetic differences in phenological responses to climate warming are still largely unclear. Third, phenological responses to experimental and natural conditions may be significantly different. A meta-analysis reported that warming experiments underestimated phenological responses comparing with those from long-term natural observations (Wolkovich *et al.*, 2012), likely because both experiments and long-term datasets cannot effectively exclude the confounding effects from other unmeasured environmental factors (Zavaleta *et al.*, 2003).

Despite of above limitations, manipulative experiments have the advantage over natural observations that certain conditions can be kept constant (e.g. water, light, nutrients can all be controlled for), rendering them ideal for hypothesis testing and substantially deepening our understanding of phenological responses to climate change. Such knowledge is critical for improving predictions of phenology shifts, species interactions, and ecosystem carbon and water cycles.

2.5 Phenology modelling approaches

Phenology models are important tools in phenology studies (i) to investigate the response of plant phenology to future climate change (Cleland *et al.*, 2007; Liu *et al.,* 2019); (ii) to couple phenology into state-of-the-art Earth system models for exploring regional- to global-scale carbon and water cycles and energy fluxes (Krinner *et al.*, 2005); and (iii) to predict species distributions in a changing world (Chuine, 2010). Overall, previous modelling efforts have been biased toward spring phenological events and relatively fewer have been on autumn phenology.

Modelling spring phenology has a long history (Table S2). Earlier modelling studies, employing statistical approaches (i.e. empirical models), relied on the concept of "degree-days" (Reaumur, 1735) and assumed that spring phenological events occur when a certain accumulation of heat units is achieved (e.g. the Spring Warming Model (Sarvas, 1974), the Thermal Time Model (Cannell & Smith, 1983)). As future warming may exceed the past temperature range, using statistical models to estimate future phenology changes may result in considerable biases. To yield more realistic predictions, scientists have also developed more mechanistic models (i.e. process-based models) that explicitly consider the developmental phases preceding leaf unfolding (e.g. endodormancy and ecodormancy (Lang, 1987)). These mechanistic models, based on the number of model-incorporated preceding development phases, can be roughly classified into one-phase and two-phase models. One-phase models such as the ForcTT Model, the ForcSar Model (Chuine *et*

al., 1999) and the UniForc Model (Chuine, 2000) assume that leaf unfolding occurs when a critical state of accumulated forcing temperature is attained during the ecodormancy phase (Sarvas, 1974; Chuine, 2000). Two-phase models assume that a certain amount of chilling is required to break endodormancy before ecodormancy can start. Examples of two-phase models include the Sequential Model (Hänninen, 1990), the Parallel Model (Landsberg, 1974), and the Unified Model (Chuine, 2000). Some models such as the DORMPHOT Model (Caffarra *et al.*, 2011) and the Four Phase Model (Vegis, 1964) consider more developmental phases during the dormancy, as well as the effect of photoperiod. Some other theoretical models, in contrast, follow the assumption of a cost-benefit trade-off in optimizing resource acquisition during the production of leaves. For example, the Promoter-Inhibit Model prescribes various compounds that promoting or inhibiting the development of buds (Linkosalo *et al.*, 2008). The Carbon-Balance Model addresses the balance between the gains of leaf photosynthesis and costs of leaf respiration (Kikuzawa, 1991); and the Growing Season Index (GSI) Model applies several biophysical variables to simulate the seasonal variation in satellite-derived NDVI (Jolly *et al.*, 2005).

Model comparison studies have revealed several important findings (Table S2). Nonetheless, evidence that supports the outperformance of models involving two-phase leaf unfolding versus one-phase models is still limited (Melaas *et al.*, 2015; Basler 2016; Chen *et al.*, 2016). For example, models incorporating photoperiod, such as the DORMPHOT Model, perform slightly better than those driven by

temperature alone (Liu *et al.*, 2018a); whereas Basler (2016) suggested that one-phase models and more complex process models give almost the same results. Overall, current models are still underperforming, especially in large-scale plant phenology studies where species-specific phenology models are used. This is mostly because the confounding effect of factors other than temperature, such as light and water availability, could also have important impact on plant phenology but has not yet been well embedded into current phenology models.

Compared to the modelling of spring phenology, the modelling of autumn phenological events (e.g. leaf coloring and senescence) is even more challenging because processes underlying autumnal phenological events are still poorly understood (Richardson *et al.*, 2012). Autumn phenology models are usually based on either specific temperature or photoperiod thresholds (White *et al.*, 1997), or cooling degree-days (CDD, similar to the concept of "degree-days") (Delpierre *et al.*, 2009). On the other hand, recent studies have suggested that coupling the carry-over effect of leaf unfolding on leaf senescence (Fu *et al.*, 2014a) into the CDD models could improve model performance (Keenan & Richardson, 2015). Furthermore, to date, autumn phenology models have only been developed and calibrated against a limited spatial coverage of *in situ* leaf senescence records (Table S3), and thus yield a large root mean square error (RMSE) of around 10 days (Delpierre *et al.*, 2009; Jeong & Medvigy, 2014). Olsson and Jönsson (2015) suggested that using a fixed

CDD requirement might be inadequate for tree species across large regions and that other factors such as precipitation and photoperiod effects need to be considered.

Overall, despite of recent progresses in phenology modelling, there are still several important issues to be addressed in future research. First, modelling efforts need to be based on improved understanding and coupling of mechanisms regulating plant phenological events, which can be achieved using approaches like manipulative experiments. Second, performances of these models are acceptable for individual plants and at local sites (Chuine, 2000; Caffarra *et al.,* 2011). Nonetheless, scaling up from plant and site-level to regional and continental is a daunting challenge. Jeong *et al.* (2013a) was among the first to model and predict regional scale spring phenology through modifying local-scale models. It is still noteworthy, however, that local model calibration (usually at the scale of plant function type) might not be able to account for the large variation in parameters within and among species. Therefore, it is particularly important to carefully implement model parameterizations. Third, models based on the concept of "degree-days" apply the sum of temperature (ignoring the temporal variations in temperature) during a certain period, which therefore often fail to predict phenology dates under extreme climate conditions (Liu *et al.*, 2018a).

3. Evidence for - and Patterns in Recent Plant Phenological Changes

3.1 Evidence and patterns from *in situ* observations

Over the past decades, one of the most striking patterns of phenological changes is the earlier onset of spring phenological events, which has been broadly observed across Europe, North America and Easter Asia, with both satellite and ground-based (*in situ*) observations. In fact, almost all *in situ* studies reveal a spring advancement, although the amplitude of such advancement differs substantially among studies due to differences in study area, period, and studied species. For example, Chmielewski and Rötzer (2001) reported an earlier beginning of the growing season by 8 days in 1969-1998 (almost 3 days per decade), using leafing dates from 50 European International Phenological Gardens (IPGs). Fu *et al.* (2014b) reported a consistently advancing trend in leaf unfolding by 4.2 days per decade for six European deciduous tree species during 1982-2011 (based on the Pan European Phenology (Project PEP725) Network database that includes 1,001,678 phenological records, see also Figure 3a). Compared to Europe, *in situ* documented changes in spring phenology of North America were slower. Wolfe *et al.* (2005) reported an advancement of 0.5 days per decade for spring leaf unfolding of lilac in northeastern USA during the period 1965-2001. Recently, *in situ* leaf unfolding from 43 phenological stations of the USA National Phenology Network (US-NPN) also revealed an advancing trend of 0.9 days per decade for the period 1982-2011 (Figure 3b). In China, in contrast, spring phenology appears to have advanced more than in Europe and North-America. According to the phenological records of 61 site-species combinations extracted from

a meta-analysis (Ge *et al.*, 2014), spring leaf unfolding in China has advanced by 5.5 days per decade during 1982-2011 (Figure 3c).

Compared to spring phenology, fewer studies have so far documented *in situ* autumnal phenological events (e.g. leaf coloring, leaf fall) (Gallinat *et al.*, 2015). Nonetheless, available evidence predominantly points to a delaying trend in the end date of autumn, although the magnitude is much weaker than the change in spring phenology, particularly in Europe. For example, using an enormous systematic phenological network data set from 21 European countries, Menzel *et al.* (2006) found that changes in leaf coloring/fall were on average delayed by only 0.2 days per decade during 1971-2000, with only 48% of them showing delaying trends. Similar results were also obtained using the PEP725 datasets for the period 1982-2011 (0.1 days delay per decade, Figure 3b). In China, autumn phenological dates were delayed more strongly, by 2.6 days per decade in 1982-2011 (Figure 3d), as inferred from leaf senescence records from a recent meta-analysis (Ge *et al.*, 2014). In the USA, Jeong and Medvigy (2014) also found substantially delayed leaf coloring by 2.4 – 3.6 days per decade. Figure 3 summarizes key findings of spring and autumn phenology changes in Europe, China and US based on *in situ* phenology networks.

3.2 Evidence from satellite observations

Satellite-derived plant phenology proxies are usually focused on the start (SOS) and end (EOS) of the growing season, and determined from satellite-based vegetation

indices (VIs) (Cleland *et al.*, 2007). Consistent with ground observations, satellite-based studies also reveal a progressively earlier SOS over the past three decades, with different advances in different study regions, periods and methods. For example, Zhou *et al.* (2001) found that SOS in Eurasia and North America was consistently advanced by 7.0 and 8.0 days, respectively, during the period 1982-1997. Similarly, Stockli and Vidale (2004) revealed an overall earlier SOS across Europe, by 10.6 days (i.e. 5.4 days per decade), for the period 1982-2001. de Beurs and Henebry (2005) showed that SOS occurred 9.3 days earlier in North America between 1985 and 1999 and 6.7 days earlier in Europe between 1985 and 2000. For East Asia, Piao *et al.* (2006) found a 14-day earlier (i.e. 7.9 days per decade) SOS in temperate China during 1982-1999; and Jeong *et al.* (2009b) observed an earlier SOS by 7 days in East Asia during 1982-2000.

While both *in situ* and satellite observations thus showed a general trend of earlier SOS since the 1980s, some recent satellite-based studies, in contrast, suggested that the trend of advancing SOS might have decelerated or even reversed since the 2000s (i.e. warming hiatus period). For example, Jeong *et al.* (2011) found that SOS advanced by 5.2 days in 1982–1999, but only by 0.2 days in 2000-2008, averaged across the Northern Hemisphere (NH). Similarly, a slow-down in SOS advancement was observed in temperate China during the 2000s (Piao *et al.*, 2006; Cong *et al.*, 2013). Furthermore, Fu *et al.* (2014b) detected that the advancement in SOS (12.4 days earlier per decade) during the period 1982-1999 actually reversed in the

following decades (6.6 days later per decade). As a result, SOS in the NH advanced with a weak rate of 2.1 days per decade when averaged over the entire period 1982-2011 (Figure 4a).

Spatially, SOS advanced in approximately 75% of the NH, with ~ 44% of these statistically significant at P < 0.05 (dotted region in Figure 4a). Meanwhile, a delayed SOS was also found over the same period in some regions, primarily in western North America where a pronounced cooling of spring temperature has occurred since the late 1980s (Cohen *et al.*, 2012). This finding was in line with recent studies by Wang *et al.* (2015) and Park *et al.* (2018), who reported that the overall advancing SOS trend across the NH has been weakened since 2000, particularly over western North America.

With satellite data, several studies have reported a trend towards delayed EOS over the past decades. At the regional scale, delay rates of EOS trends range from 1.2 to 6.1 days per decade were consistently observed across North America (Zhou *et al.*, 2001; Zhu *et al.*, 2012), Eurasia (Zhou *et al.*, 2001), and temperate China (Piao *et al.*, 2006; Liu *et al.*, 2016a), regardless of the study periods. Averaged over the entire NH, Jeong et al. (2011) found a delayed EOS of 2.2 days per decade in 2000-2008. Similarly, Liu *et al.* (2016b) reported an overall delaying trend of EOS by 1.8 days per decades during 1982-2011, using a combination of four EOS extraction methods (Figure 4b). The spatial pattern of EOS trends was much more heterogeneous than

that of SOS, with only ~65% of the NH showing delayed EOS trends (significant in 46%, e.g. northeastern Europe, northeastern North America) (Figure 4b). Advanced EOS was found in ~35% of the NH, mainly in Siberia and arid/semi-arid regions (e.g. central Eurasia) (Figure 4b).

During the warming hiatus periods (i.e. since the early 2000s), the slowdown of climate warming has been prevalently observed across most of the globe (Easterling & Wehner, 2009; Kosaka & Xie, 2013), rendering a stall or reversal in SOS trends across the NH (Jeong et al., 2011; Barichivich et al., 2013; Wang et al., 2015). However, it is far too early to tell whether such weakening SOS trends are short-term variations or will continue into the next decades, which will need continuous monitoring and analyses with satellite observations.

4. Drivers and Mechanisms behind Recent Plant Phenological Changes

Understanding drivers and mechanisms behind the observed recent plant phenological changes is important to predict future phenological changes and their ecosystem impacts. The timing of plant phenology events is determined by various biological and environmental factors. To what extent these factors influence plant phenology, however, is largely dependent on the different developmental stages of the phenological events and on plant specific differences in life history strategies. Here, we evaluate a few key factors that control the variation and changes in plant

phenology, including temperature, photoperiod, nutrient and water availability, and the interconnections among different phenology events.

4.1 Temperature

Temperature is generally regarded as the primary control of plant phenology (Cleland *et al.*, 2007; Peñuelas & Filella, 2009; Chuine, 2010). In 1735, the pioneer phenologist Réne Antoine Ferchault Réaumur first suggested that phenological events could be linked with the accumulated temperature in the preceding season (Reaumur, 1735). Warming results in earlier spring and later autumn (Menzel *et al.*, 2006); on the contrary, cooling delays the timing of spring and advances that of autumn. However, the response of phenological events to temperature changes is largely nonlinear (Fu *et al.*, 2015). In autumn and early spring, low temperature can play a dual role in the phenological processes. First, low temperature (chilling) activates plant stress responses and stimulates plant endodormancy (Cooke *et al.*, 2012; Delpierre *et al.*, 2016), the first stage of plant dormancy (Lang, 1987). Then, a certain amount of accumulated chilling (chilling requirement) is required to break endodormancy and lead plants into the second dormant stage, i.e., ecodormancy. During the ecodormancy stage, the growth of meristem cells is stimulated and plant cell elongation accelerates under warm temperatures, that is quantified as growing degree-days (Hänninen, 2016). A certain number of growing degree-days is needed to break ecodormancy and initiate spring phenological events. Thus, temperature plays multiple roles in the control of plant phenological processes, i.e. cold

temperature induces and breaks endodormancy and warm temperature breaks the ecodormancy.

Furthermore, recent studies have shed new light on the regulative role of temperature in plant phenology. For example, it was found that spring phenology is more responsive to warming during daytime than to nighttime warming, at both species- and ecosystem levels (Piao *et al.*, 2015; Rossi & Isabel, 2017). Considering the faster nighttime warming over the past decades (Davy *et al.*, 2017), the absence of such asymmetric warming effects in models might lead to underestimations of the temperature sensitivity of spring phenology (Piao *et al.*, 2015). With further warming, Fu *et al.* (2015) reported a declining temperature sensitivity of spring leaf-out phenology across temperate tree species in Europe, likely due to associated winter warming that results in insufficient chilling (Fu *et al.*, 2015; Vitasse *et al.*, 2018) and the complex interactions between temperature and other environmental factors (Flynn & Wolkovich, 2018).

4.2 Photoperiod

Photoperiod is another critical driver of plant phenology (Körner & Basler, 2010; Flynn & Wolkovich, 2018). Photoperiod plays a key role in regulating autumn phenological events, such as leaf senescence (Cooke *et al.*, 2012). When moving from summer to autumn, the progressively reducing photoperiod, i.e. increasing night length, induces bud set and senescence when photoperiod is below a growth-permitting threshold

(Wareing, 1956). For example, the timing of leaf senescence of mature European aspens occurs on almost the same date every year, apparently due to the regulation by photoperiod (Fracheboud *et al.*, 2009). Autumnal plant phenological dependencies on photoperiod may be subject to the modulation by low summer and autumn temperatures (Delpierre *et al.*, 2009; Xie *et al.*, 2015), although such a temperature effect may be small compared to the dominant role of photoperiod (Sparks & Menzel, 2002).

Compared to autumn phenology, the photoperiod effect on spring phenological events such as leaf-out is still largely unclear (Chuine *et al.*, 2010; Körner & Basler, 2010). In temperate and boreal regions, photoperiod co-regulates the timing of leaf-out through its interaction with temperature. In recent decades, climate warming has substantially reduced winter chilling accumulation and could thus postpone spring leaf out (Fu *et al.*, 2015). Longer photoperiods later in the season may partially compensate for the insufficient winter chilling (Basler & Körner, 2014; Way & Montgomery, 2015) and thereby stimulate tree leaf-out (Chuine *et al.*, 2010). On the other hand, with warming-induced leaf-out advancement, reduced photoperiod earlier in spring may decrease the temperature sensitivity of spring phenology and thereby prevent plants from leafing out too early and thus reduce frost damage risk (Way & Montgomery, 2015; Flynn & Wolkovich, 2018). Such effects of shortened photoperiod, however, have not been well investigated and empirical evidence is still limited. It is also noteworthy that the photoperiod sensitivity of spring phenological

events might vary substantially among different species and latitudes (Zohner *et al.*, 2016).

4.3 Nutrient and water availability

Plant phenology in temperate and boreal forests may also be influenced by water and nutrient availability, although the extent of such effects is smaller than that of temperature and photoperiod (Jaworski & Hilszczański, 2013). Specifically, recent studies found that precipitation may play a key role in determining spring (Peñuelas *et al.*, 2004; Fu *et al.*, 2014c) and autumn phenology (Xie *et al.*, 2015; Liu *et al.*, 2016a), and may even lead to multiple growing cycles (Hufkens *et al.,* 2016), although direct experimental evidence remains limited. The precipitation effect on plant phenology can be explained by its indirect impacts on the thermal requirement (growing degree days, GDD or cooling degree days, CDD) for both spring and autumn phenological events (Fu *et al.*, 2014c; Hänninen, 2016). It may also be linked with the interaction between nutrient availability and soil water content (Estiarte & Peñuelas, 2015). Decreased water availability might partly eliminate the effects of nitrogen addition on plant growth in arid and semiarid regions and thus affect plant phenology (Estiarte & Peñuelas, 2015).

At high altitudes and latitudes, snow cover and snowmelt timing are two additional key factors influencing plant phenology, particularly for shrubs and grasses (Chen *et al.*, 2015). The snow effect is partially explained by the interaction between plant

phenology, soil water content, and soil temperature. When snow first melts in early spring by the strong incoming solar radiation, soil temperature is above air temperature. Some of the snowmelt water flows into the partially frozen soil, which promotes root activities even before the air temperature rises above zero (Sutinen *et al.*, 2009; Yun *et al.*, 2018) and could thus affect the timing of spring phenology.

It is also well understood how nutrient status may affect plant phenology. For example, sufficient nutrients during the growing season may enhance plant's resistance and adaptation to freezing stress, thereby postponing autumnal leaf senescence (Sakai & Larcher, 2012). Insight from recent Free Air CO_2 Enrichment (FACE) experiments also indicates that rising CO_2 concentration might significantly delay the timing of leaf senescence (Taylor *et al.*, 2007; Reyes-Fox *et al.*, 2014), probably because elevated CO_2 could mitigate the negative effect of climatic warming on water availability (Fay *et al.*, 2012). Overall, nutrient and water availability affect plant phenology processes, especially for specific ecosystems with nutrient or water limitation. However, it is still largely unclear how nutrient and water interact with other environmental factors such as temperature and photoperiod in determining plant phenological events.

4.4 Interaction among phenological events

In addition to environmental factors, biological factors also contribute to the regulation of plant phenological processes. For example, using both *in situ* observations at the

species level (Fu *et al.*, 2014b) and remote sensing-based datasets at the ecosystem level (Fu *et al.*, 2014b; Keenan & Richardson, 2015; Liu *et al.*, 2016b), recent studies found that spring and autumn phenology are positively inter-correlated. Possible underlying mechanisms for such inter-seasonal phenological correlations may be directly related to leaf traits, such as leaf longevity and programmed cell death (Reich *et al.*, 1992; Lim *et al.*, 2007). This positive spring and autumn phenological inter-correlation may be ascribed to indirect effects of environmental factors as well. For example, earlier spring phenology may increase soil water loss in early stages of the growing season, thereby increases the prevalence of summer drought (Buermann *et al.*, 2013) that may subsequently result in earlier leaf senescence. Furthermore, the interaction between spring and autumn phenological events is likely to modify phenological responses to the ongoing climate warming. The relative importance between biological and environmental factors on phenological responses to climate warming, however, needs to be further investigated.

5. Ecosystem and Climatic Impacts of Phenological Changes

5.1 Ecological implications of recent plant phenological changes

Plant phenology plays an important role in maintaining species coexistence in multispecies plant communities. This is because large variations in phenological dates help reduce resource competition among species (Beverly & Elizabeth, 1985). Climate changes have profoundly altered the timing of phenological events (Yang & Rudolf, 2010; Thackeray *et al.*, 2016), which could desynchronize seasonal

interactions among species, leading to considerable consequences for biodiversity and ecosystem primary productivity (Kharouba *et al.*, 2018; Renner & Zohner, 2018).

First, climate-induced phenology changes may reshape community structures (Yang & Rudolf, 2010) due to the diverse phenological responses of plant species to climate change. For example, a multi-site study demonstrated that the phenology of species growing in colder regions is more sensitive to climate warming than those in warmer regions (Vitasse *et al.*, 2018). The convergence of phenological events across this temperature gradient could increase gene flow across latitudes and altitudes. Furthermore, phenology changes may not just alter the interactions among plants, but also that between trophic levels (Tylianakis *et al.*, 2008; Thackeray *et al.*, 2016; Renner & Zohner, 2018). The diverse phenological sensitivities to climate change across taxa and trophic levels have been found to alter the interactions among plants and their herbivores (Tylianakis *et al.*, 2008). Shifts in the phenological synchrony of plant-animal interactions could greatly alter the structure and dynamics of plant communities; yet currently we are still far from reaching general conclusions (Kharouba *et al.*, 2018). In addition, while this review focuses on leaf phenology, it is important to note that the differentiated responses of plant reproductive phenology to climate and environmental changes may facilitate alien species invasions (Sherry *et al.*, 2007; Prevéy & Seastedt, 2014), which are known to have dire impacts on ecosystem health (Suttle *et al.*, 2007).

Second, both modelling and observational studies have shown that changes in phenology events can also considerably influence ecosystem functions like carbon cycling (Keeling *et al.*, 1996; Piao *et al.*, 2007; Piao *et al.*, 2008). For instance, using FluxNet data, Falge *et al.* (2002) found that the extension of the growing season length increases annual gross primary productivity (GPP) by approximately 8 g C m^{-2} d^{-1} for temperate and boreal deciduous forests, and by approximately 5 g C m^{-2} d^{-1} for boreal conifer forests. Modelling studies have shown that an extension of 1-day in growing season length can increase annual GPP of northern ecosystems by 0.5-0.6 % (Piao *et al.*, 2007; White *et al.*, 2009). In fact, the linkage between phenology and the terrestrial carbon cycle has been important for understanding the mechanisms underlying the increasing vegetation activity and carbon sink in the NH observed over the past several decades (Zhu *et al.*, 2016; Piao *et al.*, 2018). For example, Piao *et al.* (2007) showed that the lengthening of vegetation growing season duration is a primary contributor for the enhanced vegetation productivity observed in northern ecosystems since the 1980s.

Because soil carbon decomposition increases concurrently with warming-enhanced vegetation productivity, an extension of growing season length does not necessarily augment ecosystem net carbon uptake, particularly in arctic ecosystems (Piao *et al.*, 2008). In general, an earlier spring enhances ecosystem net carbon uptake in the northern high latitudes as a result of a greater increase in photosynthetic carbon gain than in ecosystem respiration induced by spring warming (Keeling *et al.*, 1996). In

contrast, a warming-induced delayed autumnal senescent is likely to increase net carbon losses for arctic ecosystems, because warming-induced increases in respiratory carbon losses exceed of the increases in photosynthetic carbon gains (Piao *et al.*, 2008). These contrasting ecosystem carbon effects of phenology changes between spring and autumn can be attributed to the different environmental conditions between the two seasons. In spring, solar radiation is abundant and moisture conditions are typically optimal for vegetation productivity (Smith *et al.*, 2004). In addition, while eliciting earlier leaf emergence, warming does not strongly increase soil respiration because of the low soil temperatures in these northern ecosystems (Randerson *et al.*, 1999). The effects of phenological changes on the carbon cycle, however, may change under rapid climate warming (Piao *et al.*, 2017; Liu *et al.*, 2018b). For example, a recent study found that the positive effect of rising spring temperature on carbon uptake in northern ecosystems has significantly decreased (Piao *et al.*, 2017), probably due to the decline of temperature sensitivity of spring phenology (Fu *et al.*, 2015). This finding highlights the importance of integrating information from field experiments, surface observing networks, satellite observations, and mechanistic modelling to assess the relationship between phenology and the carbon cycle, and to elucidate how it may respond to climate change in a warmer world.

5.2 Climatic feedbacks of recent plant phenological changes

As plant phenology plays a fundamental role in controlling seasonal dynamics of water and energy exchanges between terrestrial ecosystems and the atmosphere (Peñuelas & Filella, 2009), climate change-induced plant phenological changes can in turn feed back to climate. Higher foliage cover is accompanied by simultaneous increases in canopy conductance (i.e., increased transpiration rates), altered albedo (i.e., less shortwave radiation absorbed by the canopy), and increased surface aerodynamic roughness (which facilitates the development of turbulence and the transfer of sensible heat to and from the atmosphere) (Richardson *et al.*, 2013). The rapid changes of these plant and ecosystem biophysical properties during leaf emergence or senescence can translate to abrupt changes in surface water fluxes and in the energy partitioning between sensible and latent heat (Moore *et al.*, 1996). For example, a rapid decrease in the ratio of sensible to latent heat after leaf-out causes a cooling effect that may effectively suppress the concurrent springtime temperature rise (Schwartz & Karl, 1990; Moore *et al.*, 1996). The pivotal role of plant phenology in controlling seasonal patterns of surface water and heat fluxes also indicates that warming-induced phenological shifts may, to some extent, have altered the seasonality of surface climate.

There is also an increasing body of observation-based evidence that plant phenological shifts may influence the water cycle (Kim *et al.*, 2018). Specifically, plant phenological changes may alter soil moisture, runoff, and precipitation, primarily

through influencing evapotranspiration (ET, a sum of plant transpiration, soil evaporation, and canopy interception) (Figure 5). Along with the longer presence of green cover, transpiration through open stomates and evaporation from canopy surfaces (i.e. interception) both increase (Figure 5a, b). Soil evaporation typically decreases owing to reduced solar radiation penetrating closed canopies, but this is only a minor component of the water cycle. When soil water supply is not limited, ET will substantially increase with advanced spring leaf-out (Figure 5a) and subsequent vegetation growth (i.e., a larger maximum green cover, typically in summer, Figure 5b), leaving noticeable imprint on soil moisture and river discharge (Huntington, 2008) (Figure 5). For example, Kim *et al.* (2018) reported that the earlier onset of vegetation green-up in a catchment dominated by temperate deciduous forests significantly increased ET and led to a decrease of river discharge. Meanwhile, the water cycle effect of delayed autumn leaf senescence is much smaller in magnitude, probably because of the primary limitation of ET by soil moisture supply during the vegetation senescence season. Furthermore, the water cycle effect of plant phenological changes seems to be highly dependent on the stages of plant phenology (leaf out, active growth, senescence, or dormancy) and the background climate.

Plant phenological changes can also produce extra biological forcing on surface temperature by directly modifying surface conductance and albedo, and by indirectly influencing cloud formation (Figure 5). Earlier emergence of the green canopy in spring can absorb a larger amount of solar radiation that tends to heat the canopy

surface. This mechanism is especially important for snow-covered boreal regions due to the large contrast between snow albedo and new-leaf albedo (Loranty *et al.*, 2014). In the meantime, the pronounced increase in ET that releases more absorbed energy to the atmosphere, together with the increasing cloudiness that reduces the shortwave radiation reaching the land surface, leads to a cooling effect. Whether the net impact of phenological changes on surface temperature leads to warming or cooling depends on the relative importance of all these feedback mechanisms. In East Asia, for example, Jeong *et al.* (2009a) diagnosed a strong negative correlation between spring vegetation growth and the rate of concurrent surface temperature rise. Using climate model simulations with and without coupling spring vegetation dynamics, Jeong *et al.* (2009a) found that earlier vegetation growth creates a cooling effect due to strong vegetation-evapotranspiration feedbacks.

Importantly, although earlier plant phenology may reduce surface temperature in spring and early summer through enhancing evaporative cooling (Figure 5a, b), this cooling effect may disappear and switch to a warming effect later in the growing season as soil moisture stress progressively increases. Earlier increase of evaporative water loss may lead to an earlier occurrence of- and a longer duration of soil water deficits, which in turn suppresses ET, enhances sensible heat, and amplifies temperature anomalies (Fischer *et al.*, 2007; Stéfanon *et al.*, 2012). When soil moisture is already limited due to prolonged rainfall deficit, this inter-seasonal vegetation-climate feedback mechanism is expected to exacerbate already

pronounced soil droughts, and contribute to more severe and longer droughts and heat waves (Fischer *et al.*, 2007). In Europe, model-based simulations have provided indications of such a causal link, showing that earlier phenology-induced soil moisture deficit triggered further feedbacks to the atmosphere and amplified the intensity and duration of the 2003 Europe summer heatwave (Stéfanon *et al.*, 2012).

6. Challenges and Future Directions

So far, we have provided an extensive review on recent changes in plant phenology, their drivers and mechanisms, and their ecological implications and climatic feedbacks. The synthesis of current knowledge highlights the rapid progress in the research of plant phenology over the past decades. Despite these important findings and progresses, however, there are still some critical challenges that need to be tackled in future research.

First, the performance of current phenology models is far from satisfactory. Currently, phenology models use observed phenological records, such as the date of leaf-out or remote-sensing-derived SOS, as the only biological data. Underlying mechanistic processes governing phenological events are rarely incorporated into models or only empirically represented via statistical relationships. The absence of process representation, however, induces large uncertainties when predicting phenology responses to future climates, and thereby also in global carbon, water and energy balance simulations. Future research using inverse modelling approaches with

climate manipulation experiments may help resolve this problem. Inverse models consider underlying ecophysiological and morphological processes of phenological changes. Meanwhile, ecophysiological and phenological responses observed in climate manipulation experiments can help constraining the parameters of the inverse models. To date, most climate manipulation experiments focusing on phenological responses have been conducted in boreal and temperate forests, with considerable inconsistencies in experimental settings (Chuine *et al.*, 2010; Hänninen, 2016). Many key questions remain to be answered, such as how photoperiod interacts with chilling and forcing, whether the effects of chilling and forcing occur sequentially or in parallel, and when the ecodormancy period starts and buds become responsive to warm temperatures. Chilling, forcing and photoperiod (and/or insolation) also play a role in the control of phenology in subtropical trees (Chen *et al.*, 2017), yet no focused experiments have to date been conducted in subtropical regions. It is unclear to what extent these factors and processes contribute to the regulation of the phenology of subtropical trees and whether observations from temperate trees can be extrapolated to the sub-tropics. More climate manipulation experiments, particularly but not only in subtropical regions, are needed to explicitly understand the key processes governing plant phenological dynamics, and to improve their modelling.

Second, it remains a grand challenge to scale up plant phenology from species to the landscape level. The phenological phases observed by remote sensing-based landscape scale approaches and by *in situ* species-level observations can be

different (White *et al.*, 2009; Jeong *et al.*, 2013b). Recent development in near surface remote sensing approaches, such as phenology cameras and UAV, provides some connections linking the ground- and satellite-based phenology dates. However, techniques of extracting landscape-level phenology using these new approaches and scaling-up methods are still premature. Methods of multiple-scale and spatial-temporal data fusion are urgently needed to improve the coherent representation of plant phenology across different scales. Furthermore, research on the ecological implications of phenology variations focuses largely on the species level. With the reported asynchronous phenology changes among interacting species, it is still unclear how observed phenology changes may affect their population dynamics (Forrest & Miller-Rushing, 2010) and the consequent impacts on landscape-level ecosystem structure and functions. Many questions remain unanswered, such as how species-specific phenological processes can be represented at the landscape level, and how the mismatch in phenology among species may affect landscape plant phenology.

Third, little is known about phenology of tropical forests. Satellite-based sun-induced chlorophyll fluorescence (SIF) and microwave imagery may provide alternative approaches to the investigation of tropical plant phenology. SIF and microwave analogues of vegetation index (e.g. the vegetation optical depth, VOD) are sensitive indicators of changes in canopy photosynthesis and water content (Guan *et al.*, 2012; Yang *et al.*, 2015), and have been applied to track forest phenology in the Amazon

(Jones *et al.*, 2014) and other tropical regions (Jones *et al.*, 2011; Joiner *et al.*, 2014). The relative shorter time span (e.g. since 2007 for Global Ozone Monitoring Experiment 2 (GOME-2) SIF and since 2002 for Advanced Microwave Scanning Radiometer-EOS (AMSR-E) VOD) and their coarser spatial resolution (e.g. 0.5° for GOME-2 SIF and 0.25° for AMSR-E VOD) are currently major drawbacks. However, further progress in remote sensing technologies (e.g. finer sensors) will enable us to better represent the dynamics in tropical forest phenology.

Fourth, systemic studies linking the above- and below-ground phenology are needed. Plant phenology studies largely focuses on above ground phenology, while only a handful of studies have investigated root phenology (Steinaker & Wilson, 2008; Radville *et al.*, 2018). Root production accounts for 33-67% of the terrestrial net primary production (Abramoff & Finzi, 2015), and the response of root phenology to climate change may be substantially different from that of aboveground phenology (Blume-Werry *et al.*, 2016). However, the influence of environmental changes on the timing of root growth and environmental controls of root phenology are not well understood. Radville *et al.* (2018) found that temperature might be not a primary control of root phenology in Arctic graminoid and shrub communities, since root phenology was not responsive to warming treatments. More investigations of root phenology are required to improve our understanding of root phenology processes and their main determinants, and the synchrony or de-synchronization between leaf and root phenology under climate change. Filling such knowledge gaps will enhance

our capacity in understanding and predicting plant phenological changes under ongoing anthropogenic climate change.

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Supporting Information Captions

Table 1. Major historical events in the development of plant phenological studies and their references.

Table 2. List of different spring phenology models summarized from the published literatures.

Table 3. List of different autumn phenology models summarized from the published literatures.

Figure legends

Figure 1. Major events in the development of plant phenological observations, experiments and modelling (Table S1 provides a detailed list of references for these key events).

Figure 2. A sketch map showing the observation, validation and scaling up of plant phenological data. The validation of satellite phenology retrievals and the scaling-up of ground-based data and near surface phenological observations are conducted using multiple scale/method phenological observations and spatial-temporal data fusion.

Figure 3. Histograms of phenological trends in Europe and the US. All temporal trends (1982-2011, time series 15+ years) of spring and autumn phenological events were calculated as the linear regression against time. For Europe, leaf unfolding (i.e. first visible leaf stalk, **a**) and leaf senescence (i.e. 50% of autumnal coloring, **b**) were extracted from the Pan European Phenological Database (PEP725, http://www.pep725.eu/). For China, *in situ* leaf unfolding (i.e. first leaf, **c**) and leaf senescence (i.e. beginning and 50% of autumnal coloring, **d**) phenological records were extracted from the meta-analysis by Ge et al., 2014. For the US, only the leaf unfolding dates (i.e. first leaf, **e**) were included in this analysis, because there were no sufficient records for leaf senescence in the USA National Phenology Network

(US-NPN, https://www.usanpn.org/results/data). The inset of each subplot indicates the spatial distribution of phenological stations involved in this analysis.

Figure 4. Changes in satellite-derived start (SOS, a) and end dates of the growing season (EOS, b) over the period 1982-2011. Dots in the subplots indicate significant changes in SOS/EOS. To avoid the potential interference of non-vegetation signals and human activities, we excluded regions dominated by bare soil/sparse vegetation (i.e. annual mean NDVI lower than 0.1, see Zhou *et al.* (2001)) and croplands (referred from MODIS Landover classification product (IGBP) classification). SOS and EOS were estimated using the latest GIMMS NDVI$_{3g.v1}$ dataset as the average of four methods. Modified from Liu *et al.* (2016b).

Figure 5. The biophysical feedbacks of plant phenological changes on land surface-atmosphere exchanges. In this schematic illustration, the symbol "−" ("+") in each bracket represents a positive (negative) forcing imposed on the corresponding diagnostics, from the plant phenological changes. Abbreviations of "LE", "DAS" and "LAImax" denote legacy effect, delayed autumn senescence and summer maximum vegetation cover, respectively. The shift from the shaded to the colored figures in **a** and **c** represents warming-induced changes in plant phenology.

Multi-scale/method phenological observation

Landscape

Community

Individual

Remote sensing

UAV

Phenocam

Flux tower SIF, spectra

Human observation

Spatio-temporal data fusion

Data source

Validation, Scaling-up

Spatio-temporal data fusion model

High temporal, but low spatial resolution (e.g. MODIS)

High spatial, but low temporal resolution (e.g. ETM)

High spatial and temporal resolutions

(a) Spring

Cloud (+)

Precipitation (+)

Latent heat (+)
Transpiration (+)

Albedo (−)

Evaporation (−)
Sensible heat (−)

Runoff
Soil moisture
Legacy effect (LE)

(b) Summer

Cloud (?) ⟨ LAImax (+)
            LE (−)

Precipitation (?) ⟨ LAImax (+)
                     LE (?)

Latent heat (?) ⟨ LAImax (+)
                   LE (−)

Transpiration (+) ⟨ LAImax (+)
                     LE (−)

Albedo (−)

LAImax (−)
LE
Evaporation
Sensible heat ⟨ LAImax (−)
                 LE (+)

Runoff ⟨ LAImax (−)
          LE
Soil moisture ⟨ LAImax (−)
                LE
Legacy effect

(c) Autumn

Cloud (?) ⟨ DAS (+)
            LE (−)

Precipitation (?) ⟨ DAS (+)
                     LE (−)

Latent heat (?) ⟨ DAS (+)
                   LE (−)

Transpiration (+) ⟨ DAS (+)
                     LE (−)

Albedo (−)

Evaporation ⟨ DAS (−)
              LE (−)
Sensible heat (?) ⟨ DAS (−)
                    LE (+)

Runoff ⟨ DAS (−)
          LE
Soil moisture ⟨ DAS (−)
                LE
Legacy effect

Dormant
season

←— Advanced spring leafing ----------------- Increasing maximum LAI ----------- Delayed autumn senescence (DAS) —→
                                              (summer)