PHENOLOGY



Phenology is the study of periodically recurring patterns of growth and development of plants and animal behavior during the year and how these are influenced by seasonal and interannual variations in climate, as well as habitat factors (such as elevation). Examples include the date of emergence of leaves and flowers, the first flight of butterflies, the first appearance of migratory birds, the date of leaf coloring and fall in deciduous trees, the dates of egg-laying of birds and amphibia, or the timing of the developmental cycles of temperate-zone honey bee colonies.

Because many such phenomena are very sensitive to small variations in climate, especially to temperature, phenological records can be a useful proxy for temperature in historical climatology, especially in the study of climate change and global warming.

We are interested in Phenology from two points of view, in order to provide:

- (A) a longer historical baseline than instrumental measurements, mostly based on written records;
- (B) high temporal and spatial resolution of ongoing changes related to global warming.

CRITICAL APPLICATIONS OF PHENOLOGY INCLUDE:

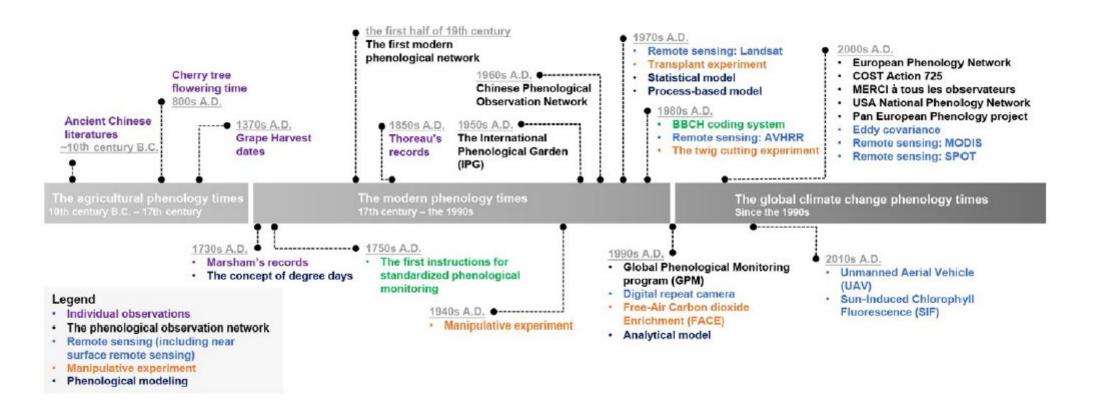
- Assessment of the vulnerability of species, populations, and ecological communities to ongoing climate change
- Understanding the timing of ecosystem processes, such as carbon cycling
- Optimization of when to plant, fertilize, and harvest crops
- Management of invasive species and forest pests
- Predictions of human health-related events, such as allergies and mosquito season
- Others....

The long history of Phenology can be roughly divided into three major periods.

The **first period** (~10th century 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. Statistical models between the timing of phenological events and climatic factors were developed, and new experiments were conducted to understand mechanisms underlying observed phenological patterns and variations. Also, very soon, phenology observation networks started to be set up across the globe, thanks to the cooperation between scientists and amateurs.

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 modeling approaches has greatly stimulated the rapid progress of phenology studies.



Major events in the development of plant phenological observations, experiments, and modeling (From Piao et al., *Glob Change Biol.* 25:1922–1940, 2019.

Observations of phenological events have provided indications of the progress of the natural calendar since ancient agricultural times. Many cultures have traditional phenological proverbs and sayings which indicate a time for action. More interestingly, historical records may, in principle, be capable of providing estimates of

The economy of entire countries and towns were based on agricultural products, and therefore we can find a lot of very precise records in diaries or historical archives concerning trades, taxes

climate at dates before instrumental records became available.

For example, the harvest dates of the **pinot noir grape in Burgundy** have been used in an attempt to reconstruct spring—summer temperatures from 1370 to 2003: The reconstructed values during **1787–2000** have a correlation with Paris instrumental data of about 0.75.

In Japan and China the time of blossoming of cherry and peach trees is associated with ancient festivals and some of these dates can be traced back to the eighth

century.





Kitao Shigemasa's eighteenth-century *hanami* (flower viewing) party scene shows three women and a man at Asukayama Park—opened by Japanese Shōgun Tokugawa Yoshimune (1684–1751), who had its famous cherry trees planted there in 1720.

Terminology and some history concerning Phenology

The word Phenology is derived from the Greek $\phi\alpha$ ($\nu\omega$ (**phainō**), "to show, to bring to light, make to appear" + λ 6 ν 0 ν 0 (**logos**), amongst others "study, discourse, reasoning" and indicates that phenology has been principally concerned with the dates of first evidence of biological events in their annual cycle.

The term was first used by Charles François Antoine **Morren**, a <u>professor of botany</u> at the University of Liège (Belgium). Morren was a student of Adolphe Quetelet. Quetelet made plant phenological observations at the Royal Observatory of Belgium in Brussels. He created a network over Belgium and Europe that reached a total of about 80 stations in the period 1840–1870 for observing Periodical Phenomena' (Observations des Phénomènes périodiques); most of the work was later extended to botanical gardens and living plant collections.

Morren participated in 1842 and 1843 in Quetelet's work, and at first suggested to mention the observations concerning botanical phenomena 'anthochronological observations', a term already introduced in 1840 by Carl Joseph Kreutzer. But later on, (16 December 1849) Morren introduced the term 'phenology' for the first time in a public lecture at the Royal Academy of Science, Letters and Fine Arts of Belgium in Brussels, to describe "the specific science which has the goal to know the "manifestation of life ruled by the time".

The founding father of modern phenological recording was **Robert Marsham**, a wealthy landowner of Stratton Strawless, Norfolk, England. From **1736** onwards he kept systematic records of "Indications of spring". These took the form of dates of the first occurrence of events such as flowering, bud burst, emergence or flight of an insect.

Generations of Marsham's family maintained consistent records of the same events or "phenophases" over unprecedentedly long periods of time for the same site (the family's mansion), eventually ending with the death of Mary Marsham in **1958**, so that trends can be observed and related to long-term climate records.

The data of oak-leafing collected by the Marshams show significant variation in dates which broadly correspond with warm and cold years. More, interestingly, their data confirm that between 1850 and 1950 a long-term trend of gradual climate warming is observable, since the recorded data of oak-leafing tended to become earlier.



In England, towards the end of the 19th century the recording of the appearance and development of plants and animals became a national pastime, and between 1891 and 1948 the Royal Meteorological Society (RMS) organised a programme of phenological recording across the British Isles. Up to 600 observers submitted returns in some years, with numbers averaging a few hundred. During this period 11 main plant phenophases were consistently recorded over the 58 years, and a further 14 phenophases were recorded for the 20 years between 1929 and 1948 for 25 plant species over the country.

The returns were summarised each year in the Quarterly Journal of the RMS as The Phenological Reports.

Jeffree (1960) summarised the 58 years of data, which show that flowering dates could be as many as 21 days early and as many as 34 days late, with extreme earliness greatest in summer-flowering species, and extreme lateness in spring-flowering species.

In all 25 species, the timings of all phenological events are significantly related to temperature, indicating that phenological events are likely to get earlier as climate warms.

With the closure of *The Phenological Reports* in 1948, Britain remained without a national recording scheme for almost 50 years, just at a time when climate change was becoming evident. More recently, a British national recording program was resumed in 1998 and, from 2000, has been led by the **citizen science project Nature's Calendar**, run by the Woodland Trust and the Centre for Ecology and Hydrology.

Also in continental europe, scientists and amateurs were involved in taking notes of the rhythms of Nature.

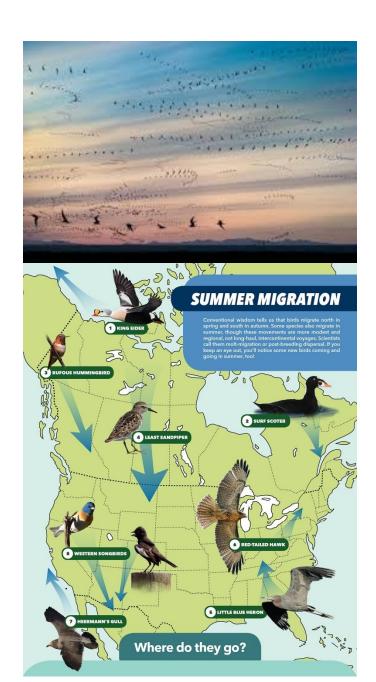
In Geneva, Switzerland, the opening of the first leaf of an **official horse chestnut tree** (*Aesculum hippocastanum* L.), originally located on the Promenade de la Treille, has been observed and recorded since 1818, thus forming the oldest set of records of phenological events I that country. The tree chosen in 1818 died at the beginning of the 20th century, and a new tree was chosen in 1905. After its death in 1929, a third tree was chosen, which died due to a fungus infection shortly after the last record, on 13 March 2015. A fourth tree was chosen in September 2015, just across the Tour Baudet de l'Hôtel de Ville, the seat of government in Geneva since 1488.

The task of observing the tree is conducted by the secretary of the Grand Council of Geneva (the local parliament), and the opening of the first leaf is announced publicly as indicating the beginning of the Spring.

[N.B.: Data show a trend during the 20th century towards an opening that happens earlier and earlier.]

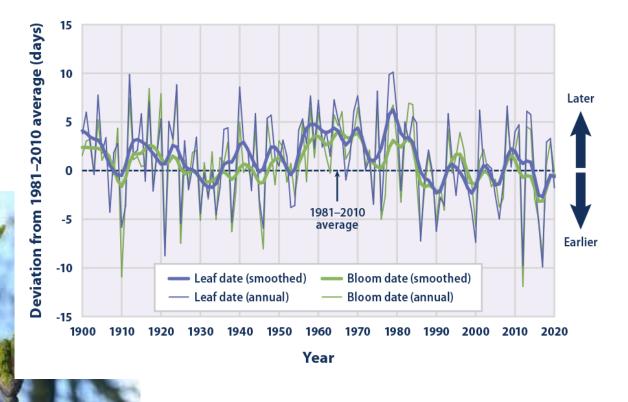


The North American Bird Phenology Program at USGS Patuxent Wildlife Research Center (PWRC) is in possession of a collection of millions of bird arrival and departure date records for over **870 species across North America**, dating **between 1880 and 1970**. This program, originally started by Wells W. Cooke, involved over 3,000 observers including many notable naturalists of the time. The program ran for 90 years and came to a close in 1970 when other programs starting up at PWRC took precedence. The program was again started in 2009 to digitize the collection of records and now with the help of citizens worldwide, each record is being transcribed into a database which will be publicly accessible for use.



In Phenology, each observation must be referred to a species, to a precise locality, and to a precise date.

Merging the data together, temporal sequences can be built, and maps can be traced, showing temporal and spatial trends for each specific stage of interest.



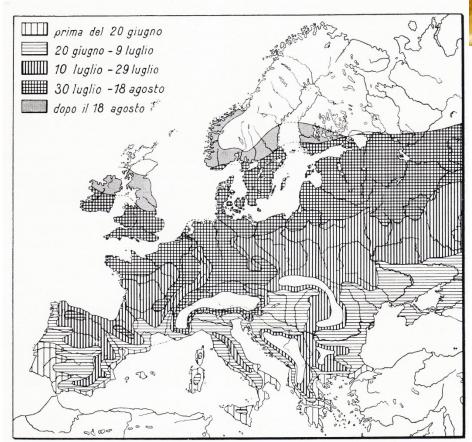
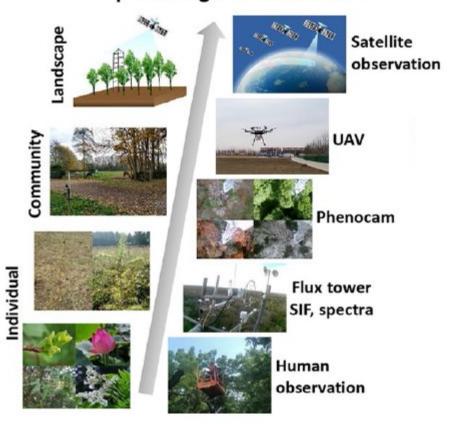


Fig. 651. — Date di mietitura del frumento in Europa (da SCHNELLE, modificata).

Multi-scale/method phenological observation



A sketch map showing the observation and scaling up of plant phenological data.

Ground-based phenology observations

Ground-based observation is a traditional, but still highly useful method in phenology studies and provides first-hand direct evidence of phenological changes.

This approach is 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, they are rare in harsh environments, such as arctic and alpine tundra ecosystems, or in arid desert ecosystems.

Uniform protocols to describe phenological events have been developed, but data interchange and integration among different regions or researchers remain problematic.

The **BBCH** (Biologische Bundesanstalt, Bundessortenamt und CHemische Industrie, DE) system is a good example that has provided a uniform definition of plant development stages.



Growth stages of mono-and dicotyledonous plants BBCH Monograph

2. Edition, 2001Edited by Uwe MeierFederal Biological Research Centre for Agriculture and Forestry

Growth stages of mono-and dicotyledonous plants

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Federal Biological Research Centre for Agriculture and Forestry

BBCH Monograph

The extended BBCH-scale

Hack et al., 1992

The extended BBCH-scale is a system for a uniform coding of phenologically similar growth stages of all mono- and dicotyledonous plant species. It results from teamwork between the German Federal Biological Research Centre for Agriculture and Forestry (BBA), the German Federal Office of Plant Varieties (BSA), the German Agrochemical Association (IVA) and the Institute for Vegetables and Ornamentals in Grossbeeren/Erfurt, Germany (IGZ). The decimal code, which is divided into principal and secondary growth stages, is based on the well-known cereal code developed by ZADOKS et al. (1974) in order to avoid major changes from this widely used phenological key. The abbreviation BBCH derives from Biologische Bundesanstalt, Bundessortenamt and CHemical industry.

The basic principles of the scale

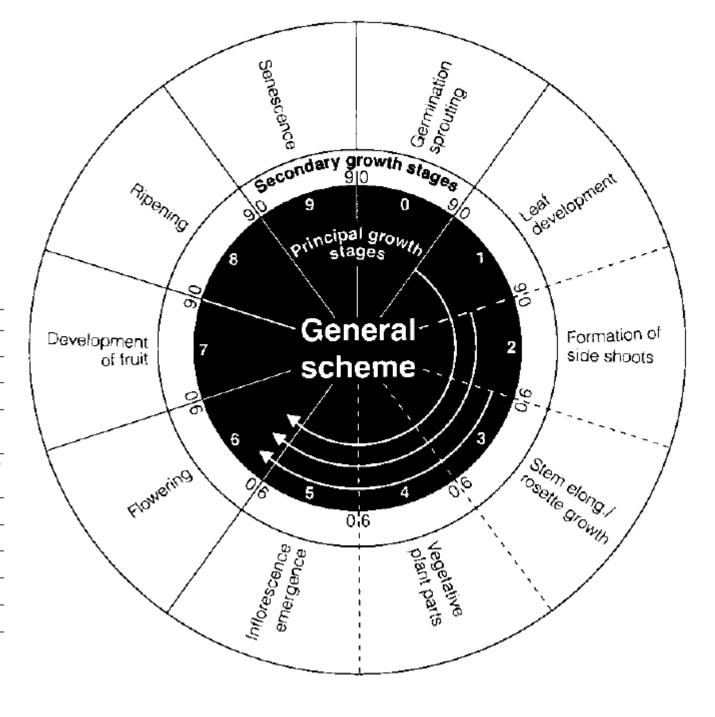
- The general scale forms the framework within which the individual scales are developed. It can also be used for those plant species for which no special scale is currently available.
- Similar phenological stages of each plant species are given the same code
- For each code, a description is given, and for some important stages, drawings are included.
- For the description of the phenological development stages, clear and easily recognised (external) morphological characte-ristics are used.
- Except where stated otherwise, only the development of the main stem is taken into consideration.
- The growth stages refer to representative individual plants within the crop stand. Crop stand characteristics may also be considered.
- Relative values relating to species- and/or variety-specific ultimate sizes are used for the indication of sizes.
- The secondary growth stages 0 to 8 correspond to the respective ordinal numbers or percentage values. For example stage 3 could represent:
 3rd true leaf, 3rd tiller, 3rd node or 30% of the final length or size typical of the species or 30% of the flowers open.
- Post harvest or storage treatment is coded 99.
- Seed treatment before planting is coded 00.

Organisation of the scale

The entire developmental cycle of the plants is subdivided into ten clearly recognizable and distinguishable longer-lasting developmental phases. These **principal growth stages** are described using numbers from 0 to 9 in ascending order (see Figures 1a and b). The principal growth stages are described in Table 1. Owing to the very many different plant species there may be shifts in the course of the development or certain stages may even be omitted.

Principal growth stages

Stage	Description
0	Germination / sprouting / bud development
1	Leaf development (main shoot)
2	Formation of side shoots / tillering
3	Stem elongation or rosette growth / shoot development (main shoot)
4	Development of harvestable vegetative plant parts or vegetatively propagated organs / booting (main shoot)
5	Inflorescence emergence (main shoot) / heading
6	Flowering (main shoot)
7	Development of fruit
8	Ripening or maturity of fruit and seed
9	Senescence, beginning of dormancy



Maize Weber and Bleiholder, 1990; Lancashire et al., 1991

Phenological growth stages and BBCH-identification keys of maize

(Zea mays L.)

07

Code	Description	
Princip	pal growth stage 0: Germination	
00	Dry seed (caryopsis)	
01	Beginning of seed imbibition	
03	Seed imbibition complete	
05	Radicle emerged from caryopsis	
06	Radicle elongated, root hairs and/or side roots visible	

Principal growth stage 1: Leaf development^{1,2}

Coleptile emerged from caryopsis

		•
10	First leaf through coleoptile	
11	First leaf unfolded	
12	2 leaves unfolded	
13	3 leaves unfolded	
1.	Stages continuous till	
19	9 or more leaves unfolded	

Emergence: coleoptile penetrates soil surface (cracking stage)

Principal growth stage 3: Stem elongation

30	Beginning of stem elongation	
31	First node detectable	
32	2 nodes detectable	
33	3 nodes detectable	
3.	Stages continuous till	
39	9 or more nodes detectable ³	

Principal growth stage 5: Inflorescence emergence, heading

	•	9	•		
51		Beginning of tassel emergence: tassel of	detectable	at top of ster	m
53		Tip of tassel visible			
55		Middle of tassel emergence: middle of t	assel begi	ns to separat	te
59		End of tassel emergence: tassel fully er	merged an	d separated	

Maize Weber and Bleiholder, 1990; Lancashire et al., 1991

Phenological growth stages and BBCH-identification keys of maize

Princi	pal growth stage 6: Flowering, anthesis	
61	Male: stamens in middle of tassel visible	
	Female: tip of ear emerging from leaf sheath	
63	Male: beginning of pollen shedding	
	Female: tips of stigmata visible	
65	Male: upper and lower parts of tassel in flower	
	Female: stigmata fully emerged	
67	Male: flowering completed	
	Female: stigmata drying	
69	End of flowering: stigmata completely dry	

Principal growth stage 7: Development of fruit

71	Beginning of grain development: kernels at blister stage, about 16% dry matter
73	Early milk
75	Kernels in middle of cob yellowish-white (variety-dependent),
79	content milky, about 40% dry matter Nearly all kernels have reached final size

Principal growth stage 8: Ripening

Description

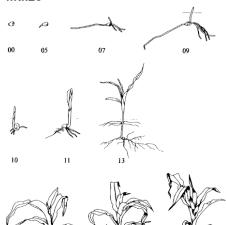
Code

83	Early dough: kernel content soft, about 45% dry matter
85	Dough stage: kernels yellowish to yellow (variety dependent),
	about 55% dry matter
87	Physiological maturity: black dot/layer visible at base of kernels,
	about 60% dry matter
89	Fully ripe: kernels hard and shiny, about 65% dry matter

Principal growth stage 9: Senescence

· · · · · · · · · · · · · · · · · · ·	growth stage of concession
97	Plant dead and collapsing
99	Harvested product

Maize









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. However, their quality is often doubtful and it remains a grand challenge to and conduct systematic big data analyses and extract phenological patterns from these data with variable quality (Mayer, 2010).

Naturens kalender

Naturens kalender



The project has the mission to collect phenological observations of plants and birds in Sweden. Observations are made by scitizen scientists thorughout Sweden of:

 Plants budburst, flowering, ripening of fruits ...

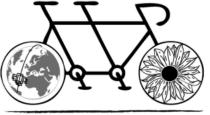


The Autumn Experiment - Höstförsöket



Climate change is impacting when the growing season in nature begins in the spring and when it ends in the autumn. Previous research has shown that changes to the climate ...

♥0 □0 **⊙**539 **<** ▼



PhenoTandem

PhenoTandem -Harmonizing Remote Sensing and Citizen Science vegetation phenology ...



The main goal of this project is to harmonize the remote sensing approach to vegetation phenology with the traditional citizen science phenological observations. This goal can be achieved by developing ...





Formal education programs

- K-12 students: start by focusing on one grade level.
- Undergraduate students: develop modules to incorporate phenology in ecology, forestry, geography, climatology, statistics.
- Graduate students: develop graduate course(s) and self-directed studies. Informal Education for general public
- Courses for adult learners and non-traditional students.
- Interpretive programs of national parks, nature centers, museums, and botanical gardens.

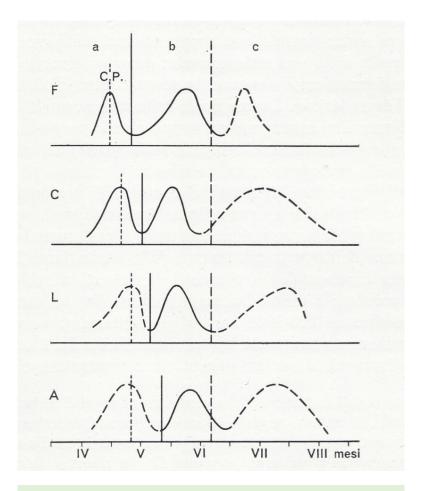
Citizen science/observer training

Engaging the general public as observers/reporters. USA-NPN can provide instructional materials via web or paper. These would include instructions for registration, selection of location to observe and species; recording of phenophases, environmental details (weather, slope, aspect, geolocation), how, when where of reporting. Other materials would be regular feedback to observers including visualization of data (graphs, charts, pictures, interactive maps, newsletters ideally twice a year). Sense of community and teamwork is enhanced through sending observers an annual list of regional observers. Recognition items can include pins, certificates, color photographs on stickers, refrigerator magnets etc.

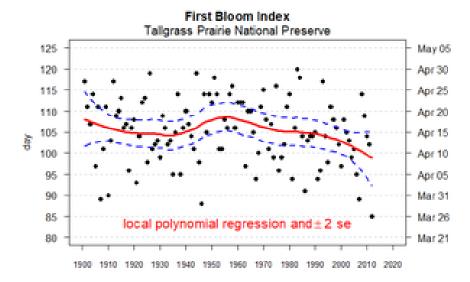
Remote Sensing & Phenology

The study of phenology of whole stands of vegetation, ecosystems and regions received considerably improvement by the development of recent technological advances in studying the earth from space. This resulted in a new field of phenological research that is concerned with observing on a global scale using proxy approaches. These methods complement the traditional phenological methods which recorded the first occurrences of individual & species phenophases. Due to the resolution of the images taken, the new approach can work better at level of plant communities when not ecosystems.

Already in the '60s of the last century, with the development of a branch of Botany devoted to the study of plant communities (phytosociology, of which plant sintaxonomy is a further lateral branch), the study of the chronochanges of single plant species moved towards that of whole plant communities: the new discipline was called **«Sinphenology»**.



Flowering phases of beech forests: F, eutrophic beech forests; C, thermophilous beech forests; L, acidophilous beech forests; A, montane beech forests. (a) first eliophytic wave; (b) second eliophytic wave; (c) sciaphylous wave; CP, gem sprouting.

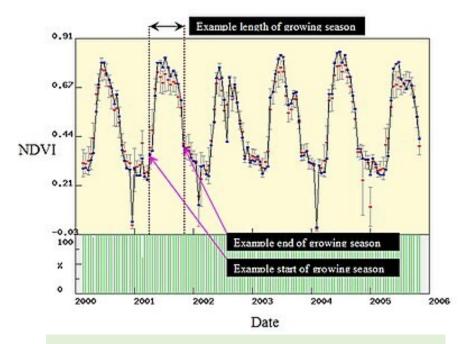


Historical day of year for first bloom index (FBI) for the Tallgrass Prairie National Preserve, Kansas (dots) fitted with a local polynomial regression model (loess in red) and a 2 standard error band (blue)

The most successful of the remote sensing approaches is based on tracking the temporal change of a Vegetation Index (like **Normalized Difference Vegetation Index**(NDVI)). NDVI makes use of the vegetation's typical low reflection in the red (red energy is mostly absorbed by growing plants for Photosynthesis) and strong reflection in the Near Infrared (Infrared energy is mostly reflected by plants due to their cellular structure).

The evolution of the vegetation index through time exhibits a strong correlation with the typical green vegetation growth stages (emergence, vigor/growth, maturity, and harvest/senescence).

The temporal curves are analyzed to extract useful parameters about the vegetation growing seasons (start of season, end of season, length of growing season, etc.). Other growing season parameters could potentially be extracted, and global maps of any of these growing season parameters can be constructed and used in all sorts of climatic change studies.



NDVI temporal profile for a typical patch of coniferous forest over a period of six years. This temporal profile depicts the growing season every year as well as changes in this profile from year to year due to climatic and other constraints.

These phenological parameters are only an approximation of the true biological growth stages. This is mainly due to the limitation of current space-based remote sensing, especially the spatial resolution, and the nature of vegetation index. A pixel in an image does not contain a pure target (like a tree, a shrub, etc.) but contains a mixture of whatever intersected the sensor's field of view.

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. 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.

Another example based on the MODIS enhanced vegetation index (EVI) showed that the Amazon Rainforest, as opposed to the long-held view of a monotonous growing season or growth only during the wet rainy season, does in fact exhibit growth spurts during the dry season: difficulties in observing what happens in the higher strata of the forest canopy easily explain these conclusions.





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, 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.

Notwithstanding these shortcomings, many phenological works based on remote sensing could show an apparent increase in vegetation productivity that most likely resulted from the increase in lengthening of the growing season in the temperate and boreal forests (for critical notes on these results, see later).

Phenology & Modeling

Phenology models are important tools in phenology studies (a) to investigate the response of plant phenology to future climate change, and (b) to couple phenology into state-of-the-art Earth system models for exploring regional- to global-scale carbon and water cycles and energy fluxes.

Most modeling efforts have been biased toward spring phenological events and relatively fewer have been on autumn phenology.

Modeling spring phenology has a long history. Earlier modeling 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)), to develop only later more mechanistic models (i.e., process-based models) that explicitly consider the developmental phases preceding leaf unfolding (e.g., endodormancy and ecodormancy), assuming e.g. that a certain amount of chilling is required to break endodormancy before ecodormancy can start.

Growing degree days (GDD), also called growing degree units (GDUs), are a heuristic tool in phenology. GDD are a measure of heat accumulation used by horticulturists, gardeners, and farmers to predict plant and animal development rates such as the date that a flower will bloom, an insect will emerge from dormancy, or a crop will reach maturity. GDD is credited to be first defined by Reaumur in 1735, a French entomologist and writer who contributed to many different fields, especially the study of insects.

Many developmental events of plants and insects depend on the accumulation of specific quantities of heat. Unless stressed by other environmental factors like moisture, the development rate from emergence to maturity for many plants and insects depends upon the daily air temperature, regardless of differences in temperatures from year to year.

Growing degrees (GDs) is defined as the number of temperature degrees above a certain threshold base temperature, which varies among crop species. The base temperature is that temperature below which plant growth is zero. GDs are calculated each day as maximum temperature plus the minimum temperature divided by 2, minus the base temperature. GDUs are accumulated by adding each day's GDs contribution as the season progresses.

GDUs can be used to: assess the suitability of a region for production of a particular crop; estimate the growth-stages of crops, weeds or even life stages of insects; predict maturity and cutting dates of forage crops; predict best timing of fertilizer or pesticide application; estimate the heat stress on crops; plan spacing of planting dates to produce separate harvest dates.

GDD are calculated by taking the integral of warmth above a base temperature, [2] T_{base} (plant type dependant, see baseline section):

$$GDD = \int (T(t) - T_{
m base}) dt$$
 (where integration is over the time period with $T(t) > T_{
m base}$).

A simpler, approximately equivalent formulation uses the average of the daily maximum and minimum temperatures compared to a T_{base} to calculate degree-days for a given day. As an equation:

$$GDD = rac{T_{
m max} + T_{
m min}}{2} - T_{
m base}.$$

If the minimum temperature T_{min} is below the T_{base} one, there exist two variants:

- ullet variant A: Do not change T_{\min} . Only if $(T_{\max}+T_{\min})/2 < T_{\mathrm{base}}$, set $(T_{\max}+T_{\min})/2 = T_{\mathrm{base}}$. The resulting GDD is 0. This can be written more compactly as: $GDD = \max\left(rac{T_{\max}+T_{\min}}{2}-T_{\mathrm{base}},0
 ight)$
- ullet variant B: Change $T_{
 m min} < T_{
 m base}$ to $T_{
 m min} = T_{
 m base}$

For example, a day with a high of 23 °C and a low of 12 °C (and a base of 10 °C) would contribute 7.5 GDDs.

$$\frac{23+12}{2}-10=7.5$$

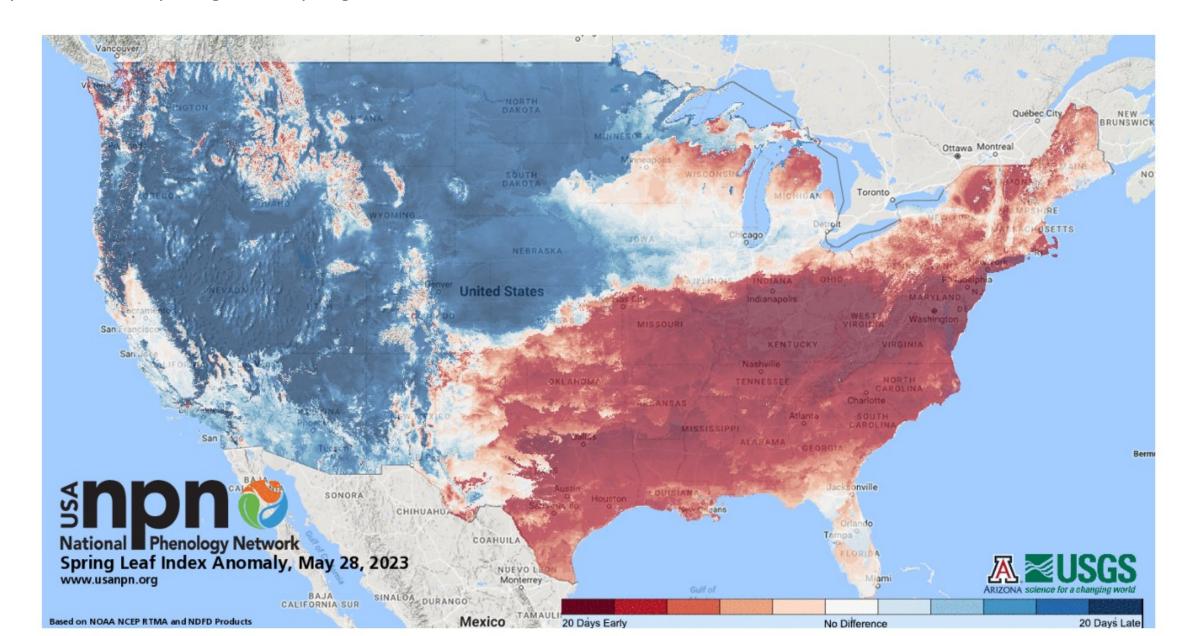
As a second example, a day with a high of 13 °C and a low of 5 °C (and a base of 10 °C) would contribute:

- version A: 0 GDD, as: $\max((13+5)/2-10,0)=0$)
- \bullet version B: 1.5 GDDs, as: (13+10)/2-10=11.5-10=1.5

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, have also important impact on plant phenology but has not yet been well embedded into current phenology models.

Therefore, it is particularly important to carefully implement model parameterizations. Finally, 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, which are becoming more and more frequent.

https://www.usanpn.org/news/spring



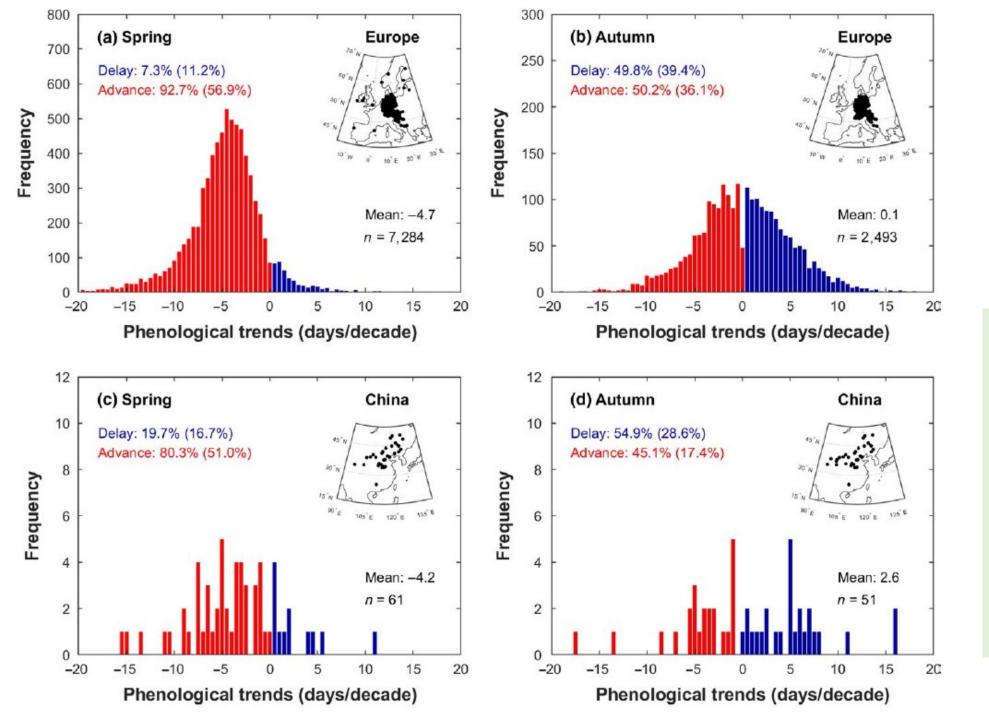
Evidence and patterns in recent plant phenology

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 ground-based (in situ) and satellite observations. 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.

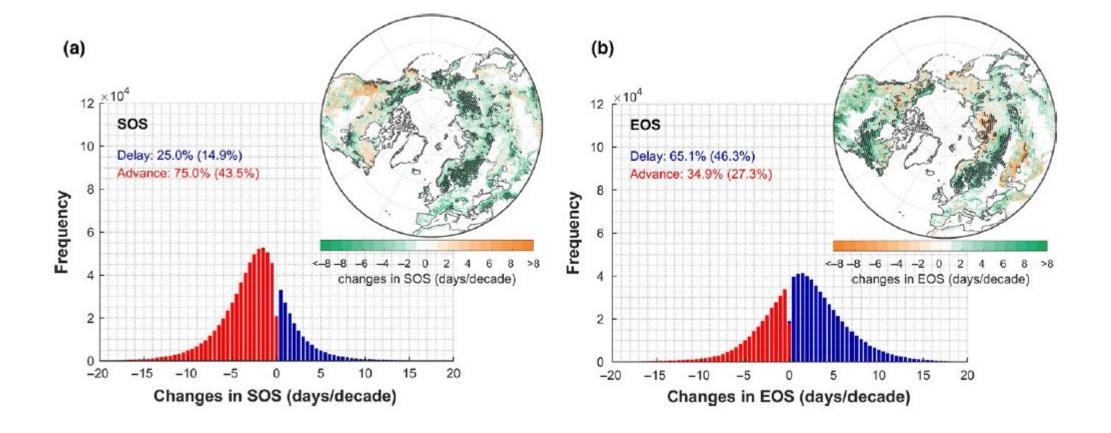




Compared to spring phenology, fewer studies have so far documented in situ autumnal phenological events (e.g., leaf coloring, leaf fall). Nonetheless, available evidence predominantly points to a delaying trend in the end date of autumn, although the magnitude is much weaker than the change in spring 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.



Histograms of phenological trends in Europe and China. All temporal trends (1982–2011, time series 15 + years) of spring and autumn phenological events were calculated as the linear regression against time. The inset of each subplot indicates the spatial distribution of phenological stations involved in this analysis



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, regions dominated by bare soil/sparse vegetation were excluded.

the COST725 initiative collected all available European phenological data (later developed as the **PEP725** database, Templ et al., 2018) and analysed more than 100,000 time series for climate change driven changes (Menzel, Sparks, Estrella, Koch, et al., 2006, hereafter referred as **GCB2006**).

The **GCB2006** study concluded that there was indeed a strong response in European phenology to climate change and that these changes matched the warming pattern.

The **GCB2006** study was also the backbone of the corresponding assessment of observed changes and responses in natural and managed systems of AR4 WGII of the IPCC (Rosenzweig et al., 2007) as well as of the subsequent paper of attribution of global impacts in nature to anthropogenic warming.

A recent case study compared the GCB2006 study extending the time-span of phenological series

Menzel et al. 2020. Glob. Change Biol.

Complete original plant phenological observation data were retrieved individually from the European Meteorological Services of Germany (DWD), Austria (ZAMG) and Switzerland (MeteoSwiss). Data of these countries account for 96.3% of the PEP database (Templet al., 2018), thus our results are comparable to any other based on PEP725 data.

	Observations	Series	Species	Phases	Stations
Germany	4,085,218	93,171	53	22	1,628
Austria	51,951	1,340	37	20	53
Switzerland	115,098	2,485	21	8	127

Out of the complete phenological data from these countries, observational data referred between **1951 and 2018** with time series (series per species/phase/station) longer than 29 years and ending in or after 2000.

Trend analyses have been conducted and compared to **GCB2006 study** obtained from the same dataset but with a different time-span of observations **(1971-2000)**

TABLE 2 Categorization of phenophases in Update comprising nine clusters and four phenological periods/seasons as compared to GCB2006

GCB2006-four phenogroups		Update-	nine clusters	Update-	-four periods/seasons
b0	Farmers' activities	F _{sp}	Sowing of spring cereals/crops (b0) and the Time per first follow-up BBCH scale (germination, leaf development, part of b1 GCB2006) phenopi	Farming Season Time period of farmers' activities from earliest phenophase in F _{sp} to the latest phenophase in F _{au} available at each station	
		F _{au}	Farmer <u>au</u> tumn Sowing of autumn cereals (b0) and the first follow-up BBCH scale before winter (germination, leaf development, part of b1 GCB2006)		Staton
b1	flowering All BBCH macrostages from 1 (leaf development, if not in F _{sp}), 2 (tillering), 3 (st				
		Cg _{sp}	Crop generative <u>spring</u> All BBCH macrostages from 5 (inflorescence emergence, heading) to 6 (flowering, anthesis) in agricultural crops		
		FWv _{sp}	<u>Fruit trees & wild plant species vegetative spring</u> All BBCH macrostages from 0 (bud sprouting), 1 (leaf development) to 3 (shoot development) in fruit trees and wild plant species		
		FWg _{sp}	Fruit trees & wild plant species generative spring All BBCH macrostages from 5 (inflorescence emergence) to 6 (flowering) in fruit trees and wild plant species		
b2	Fruit ripening	F _{su}	Farmer <u>su</u> mmer (ripeness, harvest) All BBCH macro stages from 7 (development of fruit) to 8 (ripening) in agricultural crops plus harvest dates (part of b0 GCB2006)	CgP	$\label{eq:constraint} \frac{\underline{C}\text{rop generative }\underline{P}\text{eriod}}{\text{Period from beginning of flowering in Cg}_{\text{sp}}}$ to fruit maturity stages in F_{su}
		FWg _{su}	Fruit trees & wild plant species generative summer All BBCH macrostages from 7 (development of fruit) to 8 (ripening, maturity of fruit and seed) in fruit trees and wild plant species	FWgP	\underline{F} ruit trees & \underline{w} ild plant species \underline{g} enerative \underline{P} eriod Period from (beginning of, full) flowering (FWg $_{sp}$) to fruit maturity/first ripe fruits in FWg $_{su}$
b3	Leaf colouring	FWv _{au}	Fruit trees & wild plant species vegetative autumn Phenophases related to senescence such as leaf colouring and leaf fall	GS	Growing Season Period from leaf unfolding (FWv _{sp}) to leaf colouring (FWv _{au})

Compared to the previous analsysis

There is still a clear picture of phenological advance except for autumn. For the vegetative and generative phases of crops, fruit trees and wild plants, longer time series (30+ years in Update) led to \geq 90% advancing trends in spring (**Crop generative spring**, Fruit trees and wild plants species vegetative spring & generative spring), \geq 81% for Crop vegetative spring and Fruit trees and wild plants species generative summer, and ~75% for the farmers' activities in these seasons (spring and summer).

Although the proportion of trends that was significant increased, **mean advances of spring and summer phases decreased in the extended period beyond 2000,** especially for fruit trees and wild plants, but also to a lesser degree for crops. This confirms findings of decelerated or even reversed trends in recent years.

The moving (30 years) window approach clearly showed that spring and winter warming trends exhibited very similar variation overtime, that is, the strongest trends in the 1980–2010 period. Thus, it is more likely that a reduction in forcing conditions has driven the decrease in the advance of spring and summer phenology

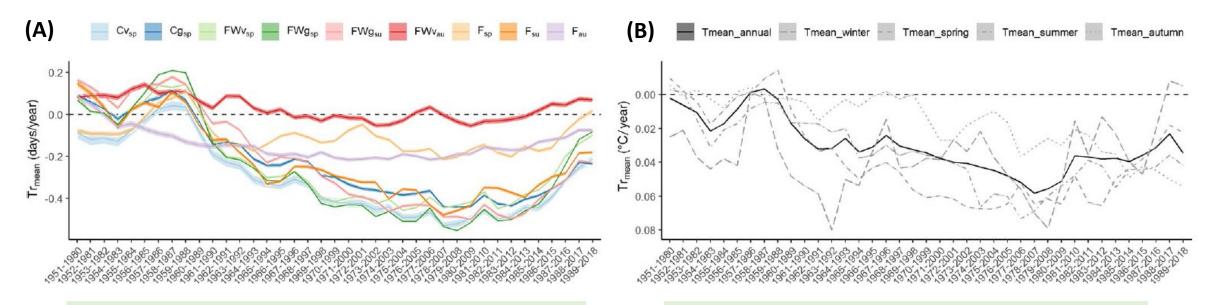


Fig. (A) - Mean slopes of linear trends (Trmean) calculated for all 15+ year phenological series in respective 30 year moving window blocks within 1951–2018 for the Update data set.

FIG. (B) - Mean slopes of annual and seasonal mean temperature trends with <u>inverted y-axis</u> for all sites and time blocks

Across the seasons the strongest advances in spring phenology were observed for early flowering species and/or very warm sites. Modelling clearly confirmed differential advances: Farmers' activities in spring and autumn only advanced at half of the rate, whereas ripening phases and especially crop vegetative phases in spring advanced more than the mean rate of ~0.22 days/year. It is important to notice that spring development of winter cereals is (at least) comparable to that of fruit trees and wild species. Non woody and insect-pollinated plant species advanced less than wind-pollinated species, which was also found in the western Mediterranean (Gordo & Sanz, 2009). Advancing trends reached their maximum rates when starting at ~1978, a finding which corresponds to the reported 1980s regime shift (Reid et al., 2016).

Although the change pattern varied over time, the (still) advancing trends could be attributed to warming. More specifically, based on percentages of significant trends matching the warming, advancing farming activities are likely, ripening phases in summer are very likely and phenological spring phases, such as leaf unfolding and flowering, are very or extremely likely to mirror the increasing temperatures.

Seasonal warming was significantly associated with spring phases' advance in fruit trees and wild plant species, generative phases in crops as well as farmers' activities mirroring winter and spring warming.

Some evidences from other disciplines...

- Long-distance migrant birds: Over the past 30 years in Oxfordshire, U.K., the average arrival and departure
 dates of 20 migrant bird species have both advanced by 8 days; consequently, the overall residence time
 in Oxfordshire has remained unchanged; the timing of arrival has advanced in relation to increasing
 winter temperatures in sub-Saharan Africa, whereas the timing of departure has advanced after elevated
 summer temperatures in Oxfordshire.
- Egg-laying dates have advanced in many bird species (Hussell, 2003; Dunn, 2004). The confidence in such studies is enhanced when the data cover periods/sites of both local cooling and warming. Flycatchers in Europe (Both et al., 2004) provide such an example, where the trend in egg-laying dates matches trends in local temperatures.
- Many small mammals have been found to come out of hibernation and to breed earlier in the spring now than they did a few decades ago (Inouye et al., 2000; Franken and Hik, 2004). Larger mammals, such as reindeer, are also showing phenological changes (Post and Forchhammer, 2002)
- Many insects, such as butterflies, crickets, aphids and hoverflies also show important phenological changes (Forister and Shapiro, 2003; Stefanescu et al., 2003; Hickling et al., 2005; Newman, 2005).
- Increasing regional temperatures are also associated with earlier calling and mating and shorter time to maturity of amphibians (Gibbs and Breisch, 2001; Reading, 2003; Tryjanowski et al., 2003).

Attention - Despite the bulk of evidence in support of earlier breeding activity as a response to temperature, counter-examples also exist (Blaustein et al., 2001).

Location	Period	Species/Indicator	Observed changes (days/decade)	References
Western USA	1957-1994	Lilac, honeysuckle (F)	-1.5 (lilac), 3.5 (honeysuckle)	Cayan et al., 2001
North-eastern USA	1965-2001 1959-1993	Lilac (F, LU) Lilac (F)	-3.4 (F) -2.6 (U) -1.7	Wolfe et al., 2005 Schwartz and Reiter, 2000
Washington, DC	1970-1999	100 plant species (F)	-0.8	Abu-Asab et al., 2001
Germany	1951-2000	10 spring phases (F, LU)	-1.6	Menzel et al., 2003
Switzerland	1951-1998	9 spring phases (F, LU)	-2.3 (*)	Defila and Clot, 2001
South-central England	1954-2000	385 species (F)	-4.5 days in 1990s	Fitter and Fitter, 2002
Europe (Int. Phenological Gardens)	1959-1996 1969-1998	Different spring phases (F, LU)	-2.1 -2.7	Menzel and Fabian, 1999; Menzel, 2000; Chmielewski and Rotzer, 2001
21 European countries	1971-2000	F, LU of various plants	-2.5	Menzel et al., 2006b
Japan	1953-2000	Gingko biloba (LU)	-0.9	Matsumoto et al., 2003
Northern Eurasia	1982-2004	NDVI	-1.5	Delbart et al., 2006
UK	1976-1998	Butterfly appearance	-2.8 to -3.2	Roy and Sparks, 2000
Europe, N. America	Past 30-60 years	Spring migration of bird species	-1.3 to -4.4	Crick et al., 1997; Crick and Sparks, 1999; Dunn and Winkler, 1999; Inouye et al., 2000; Bairlein and Winkel, 2001; Lehikoinen et al., 2004
N. America (US-MA)	1932-1993	Spring arrival, 52 bird species	+0.8 to -9.6 (*)	Butler, 2003
N. America (US-IL)	1976-2002	Arrival, 8 warbler species	+2.4 to -8.6	Strode, 2003
England (Oxfordshire)	1971-2000	Long-distance migration, 20 species	+0.4 to -6.7	Cotton, 2003
N. America (US-MA)	1970-2002	Spring arrival,16 bird species	-2.6 to -10.0	Ledneva et al., 2004
Sweden (Ottenby)	1971-2002	Spring arrival, 36 bird species	+2.1 to -3.0	Stervander et al., 2005
Europe	1980-2002	Egg-laying, 1 species	-1.7 to -4.6	Both et al., 2004
Australia	1970-1999	11 migratory birds	9 species earlier arrival	Green and Pickering, 2002
Australia	1984-2003	2 spring migratory birds	1 species earlier arrival	Chambers et al., 2005

Changes in spring and summer activities vary by species and by time of season.

Early-season plant species exhibit the strongest reactions (Abu-Asab et al., 2001; Menzel et al., 2001; Fitter and Fitter, 2002; Sparks and Menzel, 2002; Menzel, 2003).

Annual plants respond more strongly than congeneric perennials, insect-pollinated more than wind-pollinated plants, and woody less than herbaceous plants (Fitter and Fitter, 2002). Small-scale spatial variability may be due to microclimate, land cover, genetic differentiation, and other non-climate drivers (Menzel et al., 2001; Menzel, 2002).

Short-distance migrating birds often exhibit a trend towards earlier arrival, while the response of later-arriving long-distance migrants is more complex, with many species showing no change, or even delayed arrival (Butler, 2003; Strode, 2003).

Large-scale geographical variations in the observed changes are found in China with latitude (Chen et al., 2005a), in Switzerland with altitude (Defila and Clot, 2001) and in Europe with magnitude of temperature change (Menzel and Fabian, 1999; Sparks et al., 1999). Spring advance, being more pronounced in maritime western and central Europe than in the continental east (Ahas et al., 2002), is associated with higher spatial variability (Menzel et al., 2006a).

Possible consequences of altered phenology

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.

The altered timing of phenological events, caused by climate changes, could desynchronize seasonal interactions among species, leading to considerable consequences for biodiversity and ecosystem primary productivity.

Shifts in the phenological synchrony of plant—animal interactions could greatly alter the structure and dynamics of plant communities, although currently we are still far from reaching general conclusions.

Many species may experience changes in life cycle development, migration or in some other process/behavior at different times in the season than previous patterns depict due to warming temperatures. When interacting species change the timing of regularly repeated phases in their life cycles at different rates, a **mismatch in interaction timing** is derived, which may negatively harm the interaction.

Mismatches can occur in many different biological interactions, including between species in one trophic level (<u>intratrophic interactions</u>) (i.e. plant-plant), between different trophic levels (<u>intertrophic interactions</u>) (i.e. plant-animal) or through creating competition (<u>intraguild interactions</u>).

Phenological mismatches means the loss of many biological interactions and therefore ecosystem functions are also at risk of being negatively affected or lost all together. Phenological mismatches will effect species and ecosystems food webs, reproduction success, resource availability, population and community dynamics in future generations, and therefore evolutionary processes and overall biodiversity.



A hummingbird visiting and pollinating a flower. If the flower blooms too early in the season, or if the humming bird has a delay in migration, this interaction will be lost.

For example, if a plant species blooms its flowers earlier than previous years, but the pollinators that feed on and pollinate this flower does not arrive or grow earlier as well, then a phenological mismatch has occurred. This results in the plant population declining as there are no pollinators to aid in their reproductive success.

Another example includes the interaction between plant species, where the presence of one specie aids in the pollination of another through attraction of pollinators. However, if these plant species develop at mismatched times, this interaction will be negatively affected and therefore the plant species that relies on the other will be harmed.

Bird migration, breeding, and nesting are timed every spring to coincide with the peak availability of critical food sources in a delicate synchronization that occurs across large distances and diverse habitats. If the arrival of a migrating bird to its breeding ground and the insect it depends on for food both occur two weeks earlier due to the effects of climate change, they remain in synchrony and may persist; however, if the bird arrives before or after the insect's hatch/emergence they become out of synchrony and the bird not have enough food to successfully reproduce, ultimately leading to population declines.

For instance, it has been documented that shifts in the phenology of insects in Europe have been more rapid than changes in the migratory phenology of pied flycatchers, *Ficedula hypoleuca*, leading to mistimed reproduction.



About phenological mismatch: Vulnerability of a specialized pollination mechanism to climate change revealed by a 356-year analysis.

HUTCHINGS et al., 2018. Botanical Journal of the Linnean Society, 186: 498–509.

Pollination of the early spider orchid, *Ophrys sphegodes*, by sexual deception of male *Andrena nigroaenea* bees depends on male bees emerging before female bees and before flowering, and on the orchid flowering before female bee emergence, so that competition for the services of naïve male bees is avoided







Ophrys sphegodes flowers emit a floral bouquet that strongly resembles that of virgin female A. nigroae-nea, leading to sexual deception of naïve male bees. In most years, A. nigroaenea males emerge before peak flowering in O. sphegodes. In common with many bee species (Eickwort & Ginsberg, 1980), the emergence of A. nigroaenea males also usually precedes the emergence of females, and in the temporary absence of female bees as mates, the males attempt to copulate with flowers of the orchid. In doing so, they transfer pollen from one flower to another.

Because the orchid provides no reward for the pollinator, there is no incentive for habituated bees to continue to visit orchid flowers, but variation in the chemical signature of the floral bouquet between plants is enough to mask the truth.

Pollination in O. sphegodes is strongly dependent on the temporal sequence of bee emergence and orchid flowering. Success depends on male bees emerging from winter hibernation before orchid flowering and female bee emergence, and on the orchid flowering before female bee emergence. Crucially, if flowering and female bee emergence coincide, or if female bees emerge earlier than the orchid flowers, pollination is likely to be reduced or even fail completely, because of competition between the orchid and female bees for, respectively, pseudocopulatory and copulatory services from male bees.

It was observed that yearly variation in spring temperature had markedly different impacts on the phenology of flight in male and female *A. nigroaenea*, and of flowering in *O. sphegodes*.

Four data sets were used for the study:

- (1) Data on mean monthly temperature from 1659 to 2014 were obtained from the CET record;
- (2) Data on the timing of flowering in O. sphegodes were obtained from a field-based demographic study conducted from 1975 to 2006;
- (3) Data on peak flowering of O. sphegodes between 1848 and 1958 were obtained from fully dated herbarium specimens stored at the Royal Botanic Gardens, Kew, and the British Museum, London;
- 4) Peak flying dates of male and female A. nigroaenea were obtained from fully dated museum specimens held at the Natural History Museum, London, and the Oxford University Museum of Natural History. In total, 357 specimens were included in the analysis (208 male specimens collected between 1893 and 2004; 149 female specimens collected between 1900 and 2007), with at least one specimen collected in each of 81 years in a 115-year period from 1893 to 2007.

Linear regression relationships established by Robbirt et al. (2014) between peak flying dates of male and female A. nigroaenea, peak flowering dates in O. sphegodes and spring temperature were used to predict the dates on which each of these events occurred in each of the 356 years of the CET record.

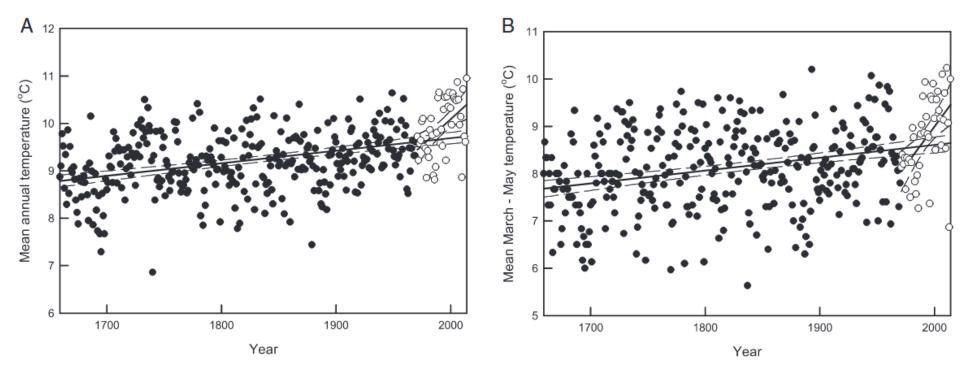


Figure 1. (A) Mean annual monthly temperature and (B) mean monthly temperature from March to May, calculated from the central England temperature (CET) record from 1659 to 2014. Mean annual monthly temperature vs. years from 1659 to 2014 (open and closed circles), y = 4.3788 + 0.00266x, r = 0.4102, $r^2 = 0.1683$, P = <0.0001, d.f. = 354, and from 1970 to 2014 (open circles), y = -34.18 + 0.02x, r = 0.526, $r^2 = 0.277$, P < 0.0001, d.f. = 44. Mean monthly temperature from March to May vs. years from 1659 to 2014 (open and closed circles), y = 3.1660 + 0.00272x, r = 0.3153, $r^2 = 0.0994$, P < 0.0001, d.f. = 354, and from 1970 to 2014 (open circles), y = -56.62 + 0.03x, r = 0.505, $r^2 = 0.255$, P < 0.0001, d.f. = 44.

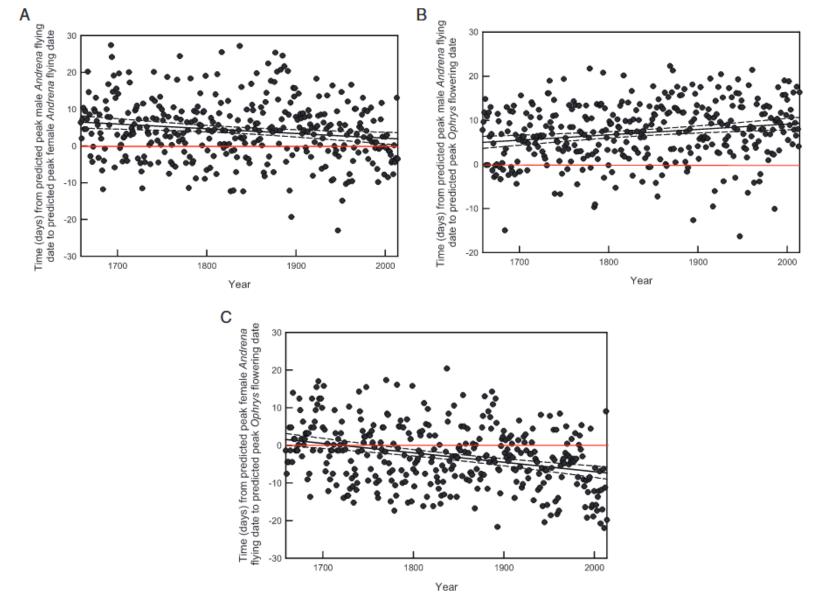
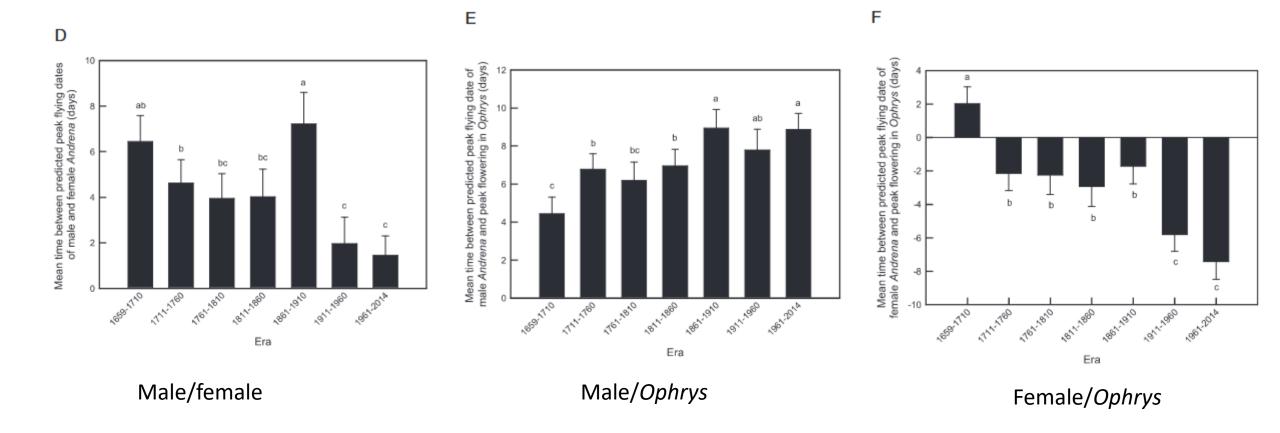


Figure 2. Time (days) between (A) predicted male and female $Andrena\ nigroaenea$ flying dates between 1659 and 2014 (y=27.915-0.013x, r=0.162, $r^2=0.026$, P<0.0001, d.f. = 354), (B) predicted male $A.\ nigroaenea$ flying date and peak flowering date in $Ophrys\ sphegodes$ between 1659 and 2014 (y=-15.204+0.012x, r=0.187, $r^2=0.035$, P<0.0001, d.f. = 354), (C) predicted flying date of female $A.\ nigroaenea$ and peak flowering date in $O.\ sphegodes$ between 1659 and 2014 (y=43.119-0.025x, r=0.315, $r^2=0.099$, P<0.0001, d.f. = 354). Positive values on the y-axis (i.e. values above the red line) indicate that the timing of the first-mentioned phenological event preceded that of the second.



Mean number of days predicted to elapse from (D) peak flying date of male Andrena nigroaenea to peak flying date of female A. nigroaenea (F6,349 = 8.12, P << 0.001), (E) peak flying date of male A. nigroaenea to peak flowering date in O. sphegodes (F6,349 = 8.08, P << 0.001), and (F) peak flying date of female A. nigroaenea to peak flowering date in O. sphegodes.

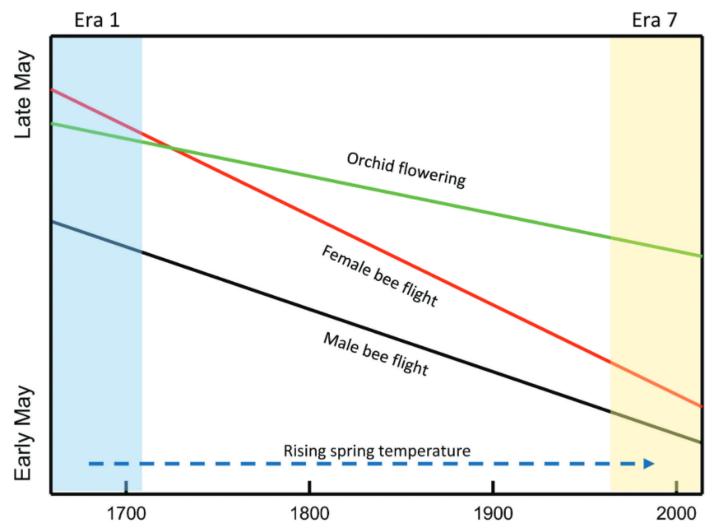


Figure 4. Schematic diagram of the predicted changes in timing of flight in male (black) and female (red) Andrena nigroaenea, and flowering (green) in Ophrys sphegodes between Era 1 (1659–1710) and Era 7 (1961–2014). All three phenological events are earlier in May in Era 7 than in Era 1 because of climate warming, but warming has the greatest impact on timing of female bee emergence and the smallest effect on timing of orchid flowering. The gradients and positions of the lines shown for each phenological event are based on the predicted effects of temperature. The time elapsing between each pair of phenological events shows gradual changes in response to warming, and the predicted sequence of the three events changes from Era 1 to Era 7. In Era 1, the mean timing of male flight precedes that of orchid flowering, which in turn (just) precedes that of female flight. In Era 7, however, male flight (just) precedes female flight, and female flight precedes orchid flowering by several days.

Conclusions

"Our results strongly support the widely expressed view that climate change threatens ecological interactions in which critical stages in the annual life cycle of one species depend on coinciding with the timing of particular stages in another. Phenological divergence caused by species responding differently both to annual weather fluctuations and to climate warming, as in the case of O. sphegodes and A. nigroaenea, clearly has the potential to disrupt such relationships."

Both modeling and observational studies have shown that changes in phenology events can also considerably influence ecosystem functions like carbon cycling.

However, contrasting ecosystem carbon effects of phenology changes between spring and autumn were observed in temperate and boreal regions of the Northern Hemisphere. This 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, whereas warming does not strongly increase soil respiration because of the low soil temperatures in these northern ecosystems. In autumn, the plants are "tired" after the high summer temperatures (often well above the mean of the period), soil temperatures are high (soil respiration is therefore higher than usual), and in some areas soil water reserves have been depleted: the CO2 balance cannot be as positive as in spring.