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**Plant phenology: definition, history,  
and response to environmental  
factors**

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## Plant phenology: definition, history, and response to environmental factors

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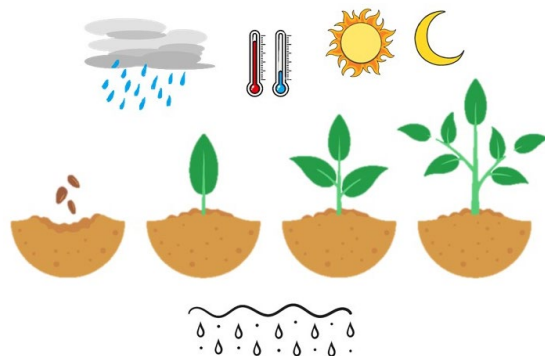
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### REVIEW ARTICLE

Plant phenology is a field of study that deals with the timing of the biological stages of plants and how they relate to environmental factors. In this review, we aim to provide a comprehensive overview of the subject, focusing on how plant phenology responds to various environmental conditions. This field has gained prominence in recent decades because of its ability to monitor the impact of climate change on plant life. It is now considered one of the most critical botanical sciences and plant breeding approaches for understanding plant adaptations to specific environments. Although environmental factors can have detrimental effects on plant growth, understanding the phenological traits of plants can help minimize their adverse effects. For example, by selecting the right sowing date for the crop, farmers, growers, and the agricultural industry can be assured of optimal growing conditions, resulting in higher profits for the agricultural industry and farmers.

**Keywords:** Plant development; phenology; climate change; yield; environmental factors



Environmental factors and climate change effect on plant growth steps

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## INTRODUCTION

Phenology studies the relationship between the stages of plant development and environmental factors (Nord and Lynch, 2009) and is a significant ecological indicator for understanding the response of plants to climate variation (Rembold et al., 2019). It is fundamental for improving plant growth and development as well as facilitating the application of agricultural management (Gregory S. McMaster et al., 2013). The phenological stage is a single point during development, such as full bloom, whereas the phenological phase is the time between two stages, such as the grain filling of wheat (Ruml and Vulic, 2005). Phenology was originally a branch of natural history and the study of species' responses to surrounding influences; however, it is currently considered an important field in climate impact research (Sparks and Menzel, 2013). Academic investigations of over a century that focused on plant phenology have led to the development of two main aspects in research related to this field: i) environmental research directed at studying the

relationship between plant evolution and environmental factors such as photoperiod and climatic constraints, including average temperatures, temperature accumulations, and humidity, and ii). evolutionary research that addressed the genetic basis and natural selection of plant phenology (reviewed by (Pachauri and Reisinger, 2008)).

Furthermore, climate change is one of the most important real challenges facing the agricultural sector, and it is a global issue discussed frequently and continuously. Global warming is caused by increased greenhouse gas (GHG) emissions into the atmosphere due to various human activities, including transport, industry, and agriculture sectors. In addition, natural disasters such as forest fires contribute to an increase in GHGs. Hence, GHGs are concentrated in the atmosphere, which allows the passage of sun rays but prevents their exit when they reflect from the earth's surface, causing an increase in the temperature. Consequently, the agricultural sector is extremely affected, as several lands are degraded and become unsuitable for agriculture. According to NASA's

Goddard Institute for Space Studies (GISS), average temperatures have increased by 1 °C since 1880, at a rate of roughly 0.15–0.20 °C per ten years (NASA, 2020b). The temperature increases from 1884 to 2019 were particularly evident (NASA, 2020a) (Figure 1).

Changes in environmental conditions are responsible for approximately 80% of the variation in production efficiency (Choudhary et al., 2019). In addition, several studies have indicated a possible decrease in agricultural production due to future potential climate change. For example, a 1.44% decrease in rainfall is expected between 2030 and 2049 in Brazil, which will reduce the current production by 18% (Pachauri and Reisinger, 2008; Choudhary et al., 2019). According to the FAO (FAO, 2017), the negative impacts of climate change will be slight until 2030, but the expected increase in temperatures, droughts, and floods will intensify thereafter. Therefore, monitoring the conditions of the agricultural sector is important for early warning and response planning to achieve agricultural sustainability and raise the level of food security.

The primary objective of this review is to obtain insights into plant phenology and responses to environmental factors. This will assist growers in matching plant phenology to the surrounding environment to increase acclimation, implement timely agricultural applications, and ultimately

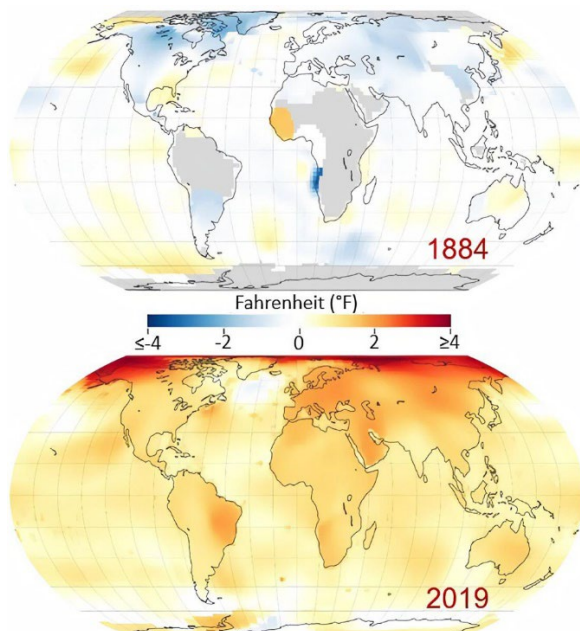
improve production efficiency. Therefore, this review begins with a definition of plant phenomenology and discusses related studies over the past century. It then describes its history, as well as the phenological observations and records used to track climate change. Finally, we explain the response of plant phenology to environmental factors, including temperature, soil moisture, and photoperiod, as well as how the date of sowing controls phenology.

## PHENOLOGY

The word “phenology” is originally derived from two Greek words: *phaino* (to appear) and *logos* (“reasoning, or rational thought”) (Ness et al., 2012). Plant phenology “studies the timing of the annual cycle of biological events and how they respond to interannual changes in the biotic and abiotic environment, particularly changes in meteorological conditions” (Shen et al., 2015). Nevertheless, all phenological definitions refer to the timing of growth, reproduction, and aging (Forrest and Miller-Rushing, 2010). Therefore, it is considered an approach that helps understand how organisms live and reproduce by adapting to the surrounding environment.

Furthermore, matching plant phenology with the environment is important for improving adaptation, leading to increased yield and reduced risks of abiotic stresses, such as drought, heat, and frost (Hunt et al., 2019; Alharbi and Adhikari, 2020). This has become an important approach in plant breeding programs. Flowering is the most important phenological stage, representing the end of the vegetative stage and the beginning of the reproductive stage. It is also highly susceptible to abiotic stress. Consequently, improving phenological traits through better adaptation to the surrounding environment will assist plants in increasing their production efficiency (Ceglar et al., 2019; Alharbi and Adhikari, 2020; Wallach et al., 2021). This approach is based on an understanding of the main environmental factors that influence plant growth. Temperature is a major factor controlling the plant growth rate, followed by humidity and photoperiod (Iannucci et al., 2008). Plant phenology is not only affected by climatic influences but also by different terrains, the characteristics of which (e.g., differences in geographical location, soil, and slope) can affect the response to environmental factors.

The effects of climate change on plants can also be determined by measuring physiological traits, such as photosynthesis and gas exchange. These measurements may require specific devices that depend on the availability of certain materials and



**Figure 1.** The change in temperature from 1884 to 2019 (NASA, 2020a) in degrees Fahrenheit. Map credit: NASA Scientific Visualization Studio.

long calibration times. Moreover, the processes might be time-consuming, and multiple devices could be required to assess the genotype response to a particular environmental factor. Plant phenology does not require specific equipment (Stokłosa et al., 2012) because it depends on phenotypic evaluation. Therefore, phenology is the simplest way to track the environmental impacts of climate change and has been supported by the Intergovernmental Panel on Climate Change (IPCC) in Switzerland (Radville et al., 2016).

Fraga et al. (2016) anticipated that climate change would significantly impact the phenology of plants in Europe in the coming decades (2041–2070), leading to alterations in leaf area, yield, and the occurrence of water stress. They also asserted that an increase in atmospheric CO<sub>2</sub> levels would partially counteract the effects of dryness, thereby promoting an increase in yield and leaf area index in Central and Northern Europe (Fraga et al., 2016). Another study analyzed linear trends in a dataset spanning 1951–2018 to determine changes in plant traits/groups across seasons and times and their attribution to warming, following the IPCC methodology. The results indicated that the negative trends were more pronounced in early spring, at higher elevations, and for nonwoody insect-pollinated species. These trends were strongly linked to winter and spring warming, resulting in a longer growing season with a constant generative period in wild plants and a shortened one in agricultural crops. Farmers' decisions differed significantly from the climate-driven phases, but their spring activities showed reinforced advancement, suggesting adaptation (Menzel et al., 2020).

New technologies for monitoring plant phenology and the impacts of climate change have been developed. Monitoring vegetation phenology is critical for determining the effects of climate change on ecosystems. Cameras are used to capture images at thirty-minute intervals, which are then uploaded to the PhenoCam server to accomplish this. These images are displayed in near real-time, and preliminary data products such as the Green Chromatic Coordinate (GCC) time series are made available to the public via the project website. This dataset is critical for validating satellite products, assessing land surface model predictions, interpreting the seasonality of ecosystem-scale CO<sub>2</sub> and H<sub>2</sub>O flux data, and investigating the effects of climate change on the terrestrial biosphere (Seyednasrollah et al., 2019).

PlanetScope imagery is another novel method that allows high-resolution monitoring of land surface phenology (LSP) in terrestrial ecosystems. This method provides daily imagery and allows the mapping of seasonal changes in surface properties. This method is extremely useful for monitoring LSP because it provides a more detailed and accurate representation of changes occurring in the ecosystem. Combining these two methods yields a comprehensive understanding of the effects of climate change on terrestrial ecosystems, which is critical for developing effective mitigation and adaptation strategies (Moon et al., 2021).

## HISTORY OF PHENOLOGY

Phenology is one of the oldest sciences that humans have studied for thousands of years to predict food availability at the beginning and end of agricultural seasons (Haggerty and Mazer, 2008). Early humans relied on their ability to identify edible plant species, optimal environments for growth, and protection methods against pests and inappropriate conditions during the growing seasons. Hence, they were sufficiently familiar with the growth stages during the vegetative (stems, leaves, and roots) and reproductive stages (flowering and fruit set) (Schaal, 2019). Consequently, they were able to increase crop productivity by determining the best agronomic practices, including sowing and harvesting dates (Russell, 1983).

Hence, plant phenology is not a modern topic, as the oldest records of plant phenology were found in 974 BC in China. The Japanese also used the phenology of cherry trees (*Prunus avium* L.) 1,200 years ago. In the 18<sup>th</sup> century, phenological changes in plants attracted the attention of botanists, and the methods of collecting data started developing either as hobbies or for study. In 1735, Réaumur proposed the first quantitative model of the temperature effect on the phenological stages occurrence, which is, nowadays and after 300 years, a fundamental component on which current phenological models depend (Chuine et al., 2013). The first suggestion for the term “phenology” was made in 1853 by the Belgian botanist Charles Morren, who also established many phenological networks throughout Europe (Delpierre et al., 2016). In the mid-18<sup>th</sup> century, Carolus Linnaeus, known as the father of modern botany and phenological observation networks (Hopp, 1974), established the first phenological network linked to botany (Philosophia Botanica "The Science of Botany"). He identified methods for classifying plants

into seasonal calendars that clarify the dates of leaf formation, flower opening, fruit production, and defoliation.

In 1918, Hopkins proposed The Bioclimatic Laws," which determine the timing of seasonal events (Miller and Keen, 2013). His proposal focused on agricultural and forestry sectors, especially in the central and western United States. Springtime was known in one of the regions but was delayed by four days for each degree of latitude to the north, every five degrees in the longitude to the east, and every 400 feet (122 m) in height. Hopkins' laws have greatly contributed to improving farmer production by providing advice for modifying agricultural practices that can increase yield or reduce exposure to biotic and abiotic stresses. For instance, he determined the optimal sowing date for winter wheat since plants may suffer from the fruit fly (*Drosophila melanogaster* Meigen) at the very early sowing stage, while a delay will expose plants to frost damage.

Although phenology is an old science (as mentioned earlier), it was not given much attention by biologists until the 1980s. Very few studies started in the 1960s, followed by a fluctuation until the beginning of the 1990s, which saw the beginning of specialized studies in plant phenology (Wolkovich and Ettinger, 2014); starting from this period research, reports, and articles related to plant phenology have been increased by about 10 times compared to in the 1980s (Tang et al., 2016). However, major interest remains in studying other plant traits such as leaf area and shape, stem diameter, and other phenotypic traits (Wolkovich and Ettinger, 2014). Therefore, the study of plant phenology requires more attention because climate change threatens the future of global natural resources.

## FACTORS AFFECTING PLANT PHENOLOGY

Environmental factors, such as temperature and precipitation, directly or indirectly control the timing of phenological events or may act as indicators that determine the internal biological clock of a plant (Forrest and Miller-Rushing, 2010). In addition, phenological changes that occur because of environmental factors differ based on the response and sensitivity of plant parts, such as leaves, stems, flowers, fruits, and the root system. For instance, light shortage causes stem elongation (Liu et al., 2016), but roots are not directly affected by light levels or photoperiod because of their presence underground. However, temperature affects the entire plant, including the shoots and roots. In general, the

response of plant phenology to a changing environment is attributed to two factors (Piao et al., 2019):

- To achieve synchronization in pollination and reproduction between individuals of a particular group,
- To avoid unsuitable conditions during the seasons in a precautionary manner.

Although there is ample evidence regarding external influences on phenological transitions (e.g., vegetative stage to flowering), these transitions are not well understood. Temperature is a major factor affecting plant phenology, but other factors, such as photoperiod and humidity, can also cause phenological changes (Moore et al., 2015). The most important environmental factors that affect plant phenology are briefly discussed in the section below.

### Temperature

The lengthy collection of phenological records (years) and historical climate reports indicate that temperature is the most important factor affecting plant phenology compared to other environmental factors (Fox and Jönsson, 2019; Lee et al., 2020). Furthermore, temperature affects biodiversity by reducing the number of organisms that cannot tolerate heat or cold. The continuous increase in global temperature disrupts natural phenological patterns in plants and other living organisms (Scranton and Amarasekare, 2017) and enhances competition between exotic plants with higher temperature tolerance than native plants. Thus, temperature increases the probability of changing vegetation cover by replacing native plants with exotic ones, resulting in the extinction of local varieties (Maiti and Maiti, 2017).

The exposure of plants to extreme temperatures for certain periods (minutes or hours) can limit their development, leading to a negative effect on phenological stages. For example, frost causes sterility and abortion of grains formed in wheat, whereas extreme heat reduces grain number and seed-filling duration (Barlow et al., 2015). In addition, exposure to 35 °C causes flower abortion in rice (*Oryza sativa* L.) (Jagadish et al., 2010), while faba bean stops flowering at 30 °C. The yield of rice, wheat, and maize (*Zea mays* L.) drops 10% with every 1 °C temperature increase. Additionally, an increase of 1 °C can minimize the yield of peas (*Pisum sativum* L.) by about 0.6 t/ha (Alharbi and Adhikari, 2020). A simulation experiment was performed on nine wheat cultivars in

two control rooms: i. room-2020, representing the current climate, and room ii. room-2070, representing the climate expected 50 years later. The results showed a short life cycle in room-2070 with an average of 10 days, as high temperatures shortened the vegetative phase and accelerated the occurrence of flowering (Sabella et al., 2020). The minimum temperature is expected to increase faster than the maximum temperature, resulting in a noticeable increase in the average daily temperature, which can determine crop yields (Meehl et al., 2007). However, understanding the response of plant growth and development to temperature changes will help improve adaptation strategies and reduce potential negative impacts (Hatfield and Prueger, 2015).

There are thermal sensors in plants (cellular components that can perceive temperature change), which enable plants to accurately sense the absolute and gradual change in daily and seasonal temperature (Bahuguna and Jagadish, 2015). Accordingly, plants respond better, leading to positive effects on phenological changes, internal tissues, and photosynthesis. Moreover, plants differ in their response to temperature based on their growth stage (germination, flowering, or fruit set), growth type (annual or perennial), and climate zone (e.g., temperate, tropical, and subtropical) (Hatfield and Prueger, 2015). Generally, phenological transformations accelerate with increasing temperature.

In contrast, low temperatures slow plant growth and delay the occurrence of various phenological stages. Several studies have demonstrated that exposure to cold stress increases the days to flowering in soybeans (*Glycine max* (L.) Merr.) (Lyu et al., 2020) and rice (*Oryza sativa* L.) (Hori et al., 2021), and flowering and maturity in wheat (Chakrabarti et al., 2011) and sorghum (*Sorghum bicolor* L.) (Amandin et al., 2020). The harm caused by low temperatures varies according to the plant species, growth stage, and surrounding conditions (Hussain et al., 2018). However, the flowering stage is the phenological stage that is most sensitive to low-temperature stress (Ohnishi et al., 2010; Chmielewski et al., 2011; Martino et al., 2021).

Not all temperature changes have negative impacts on plants. Some plants require low temperatures for a certain period to flower, and without achieving the required temperature, they may not succeed. This phenomenon is known as vernalization. The optimum temperature for most plants that require this

phenomenon ranges from 6 °C to 10 °C, whereas winter faba beans require a cooler temperature of 4 °C (Chouard, 1960).

### Soil moisture

Soil water content significantly influences plant phenology (Aikens et al., 2020). Therefore, the development of phenological stages proceeds normally when appropriate water content is available. However, stress occurs if there is a deficiency or increase in water content.

Overwatering may prevent plants from deep rooting, leading to vulnerability to falling over under high winds. Therefore, an increase in soil moisture content leads to waterlogging, resulting in rot or dead roots by blocking oxygen or providing a fertile environment for infection with fungal diseases, such as the fungus *Rhizoctonia solani* J.G. Kühn, which causes the death and fall of seedlings (Morales-Olmedo et al., 2015). In addition, an increase in soil moisture harms plant growth by limiting the physiological processes that occur in every part of the plant (Manik et al., 2019). For example, it reduces photosynthetic activity in leaves, promotes the degradation of starch and chlorophyll in stems, and decreases hydraulic conductivity in roots.

In contrast, the lack of water in the soil leads to drought, resulting in several phenological changes in shoot or root systems. Drought affects plant phenology by controlling the ratio of biomass distribution among plant parts, where a large amount of biomass is converted to roots that extend deep into the soil to obtain water (Rodrigues et al., 1995; Li et al., 2019). This distribution may occur at the expense of biomass, which is supposed to be allocated to the yield. Consequently, above-ground biomass and yield will decrease due to drought (Ivica et al., 2019). The reproductive stage (starting from flowering) is critical to the plant lifecycle and is the most susceptible to environmental conditions (including drought). Therefore, the occurrence of drought during this stage will lead to falling flowers, fruit abortion, and small seed size. Faba bean yield may decrease by approximately 79% due to drought (Migdadi et al., 2016). Phenology is related to other plant traits; hence, drought also causes changes in morphological and physiological characteristics, such as a decrease in leaf area, photosynthesis rate, chlorophyll content, and stomatal conductance (Luis Quero et al., 2006).

Moderate irrigation and determining the optimal amount for each plant are high priorities for breeding

programs. Under optimal conditions, the plant grows, develops, and produces the highest yield. Conversely, exposure to environmental stress (waterlogging or drought) harms the plant, but the damage is greater when more than one factor occurs simultaneously, such as drought and high temperature. A study on maize showed that exposure of plants to normal heat and adequate irrigation produced 1573.5 grams, whereas production decreased by 40% when exposed to drought only and 47.7% to heat only. There was a significant decrease of approximately 77.7% when plants were exposed to drought and heat together (Hatfield and Prueger, 2015). In addition, "drought followed by intense rain can increase the flooding potential, thereby creating conditions that favor fungal infestations of leaves, roots and tuber crops" (Ngoune Liliane and Shelton Charles, 2020).

### Photoperiod

Photoperiod is a major factor affecting plant phenology (Zhong Huang et al., 2001; Adole et al., 2019). It indirectly affects plant phenology through its influence on other environmental factors, such as temperature and precipitation, which ultimately control yield (Dayton, 2008). The interaction of photoperiod with other environmental factors had a great influence on the timing of phenological stages. For example, shorter photoperiods and lower temperatures during winter contribute to growth cessation and bud setting (Jackson, 2009; Soolanayakanahally et al., 2013). In contrast, long photoperiods may positively affect plant growth, leading to increased biomass production (Adams and Langton, 2005).

Several studies have focused on this aspect to determine the effects of the photoperiod on plant growth and phenology. For example, (Doust, 2017) studied the response of foxtail millet (*Setaria italica* (L.) P. Beauvois) to different photoperiod regimes. Plants exposed to a prolonged photoperiod (16/8 h light/dark) showed early flowering, high biomass production, and branching compared to those exposed to shorter periods of 12/12 h and 8/16 h (light/dark). Similar observations have been made in (*Arabidopsis thaliana* (L.) Heynh.) Plants exposed to long photoperiods show early flowering (Fernández et al., 2016) and high biomass and distribution (Dasti et al., 2002). In addition, (Singh et al., 2017) discussed a control experiment that used two photoperiod models to evaluate the effects on *Arabidopsis* flowering: a long photoperiod, long-day LD (16/8 h, light/dark), and short, short-day SD (8/16 h,

light/dark). The results showed that flowering was promoted under LD conditions but delayed under SD conditions. This was attributed to *CONSTANS* (the circadian clock-regulated gene (CO)), which is the main regulatory key to flowering and is unstable in the dark. Consequently, "the CO expression pattern provides the light-sensitive rhythmic cue required for the photoperiodic control of flowering, which depends on the coincidence between high CO levels and the light period."

Lack of light negatively affects phenological stages, leading to stem elongation (Oh et al., 2015). This phenomenon occurs because a large part of the biomass, which is supposed to be distributed fairly between the parts of the plant, is transferred to the stems to elongate and reach the light. Despite the rapid increase in length, stems are weak and have a smaller diameter than those of plants exposed to optimal conditions. Consequently, yield decreases because a large portion of the biomass allocated to yield or fruits is directed to the stems to solve the issue of light shortage, similar to the roots under drought stress. This phenomenon occurs frequently in glasshouses.

### Sowing date

The sowing date is one of the most important agricultural processes that must be considered, as it can assist plants in avoiding predicted environmental hazards (Alberio et al., 2015). For instance, sowing legumes in early May in eastern Australia is highly recommended because sowing very early (mid-April) may expose plants to the risk of frost, which may occur during the flowering time in July. Moreover, very early planting increases the risk of chocolate spots, which are caused by the fungus *Botrytis fabae* Sardiña after heavy rain. In addition, a study found that sowing chickpeas early (mid-April) in central-western and southern New South Wales, Australia, contributed to an increase in the vegetative stage, delayed flowering, decreased seed-filling duration, and ultimately low yield (Richards et al., 2020). This study concluded that the optimal selection of the sowing date is important because it controls the three most important factors that affect plant phenology: temperature, water content, and photoperiod. However, delaying planting until the end of May exposes plants to drought and high temperatures that may occur during the reproductive stage, starting in September (Matthews and Jenkins, 2020). Consequently, the sowing date plays an important

role in the timing of phenological stages and their susceptibility to environmental conditions.

Plants differ in their growth patterns in two ways: determinate and indeterminate types (Saxena et al., 2017). The determinate type of plants, such as wheat, flowers for a specific period, maybe for a week. Thus, the occurrence of any undesirable factors during the flowering period (such as drought and heat) may lead to a complete loss in yield. Therefore, flowering time, as the most susceptible stage of phenology, can avoid exposure to unfavorable environmental conditions through proper selection of the sowing date. The second pattern of growth is an indeterminate type, such as in some legume crops (e.g., faba beans and chickpeas), which, once they start flowering, continue for more than two to three months. Thus, the occurrence of an unfavorable environmental factor during the flowering period is undoubtedly less impactful than in the first type because of their long flowering period, which enables the plants to compensate in other periods.

Finally, several other factors influence plant phenology, including soil characteristics (type and texture), agricultural practices (seeding depth and plant density), and topography (height above sea level).

## SUMMARY

Plant phenology, which studies the timing of biological events and their relationship with climate, has been used to observe climate change by recording the effects of various environmental factors (e.g., temperature, soil moisture, and photoperiod) on plants. Therefore, addressing the challenges of climate change is essential. Therefore, matching plant phenology with the environment plays a vital role in increasing adaptation efficiency, performing agronomic practices at the optimum time, and ultimately achieving high yield, considering the close correlation between phenological characteristics and susceptibility to environmental factors.

## DATA AVAILABILITY

Data sharing is not applicable as no new data were generated or analyzed during this study.

## CONFLICT OF INTEREST

The authors declare that the review was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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