



REVIEW ARTICLE

Plant phenology in major forest types of India: A review

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Received: 25 June 2024; Accepted: 16 May 2025; Available online: Version 1.0: 20 November 2025; Version 2.0: 04 December 2025

Cite this article: Thasini VM, Sreekumar VB, Sreejith KA. Plant phenology in major forest types of India: A review. Plant Science Today. 2025; 12(4): 1-12. <https://doi.org/10.14719/pst.4174>

Abstract

Plant phenology has gained significant prominence due to its potential to assess the impacts of climate change on ecosystems. We documented the patterns of vegetative and reproductive phenology across major forest types in India, examined the factors influencing these patterns, identified knowledge gaps and suggested directions for future research. We collected data from published literature and followed the forest-type classification of Champion and Seth. The major forest types included in the study were moist tropical forests, dry tropical forests, montane subtropical forests, montane temperate forests, subalpine forests and alpine scrub. Summarising the phenology across Indian forest types proved to be difficult due to the lack of long-term, comparable datasets. In general, we identified that vegetative and reproductive phenology tended to be seasonal and driven by changes in abiotic variables. However, the influence of biotic factors remains largely unknown. We also highlighted the role of satellite remote sensing and near-surface remote sensing techniques in phenological research. Currently, the phenological responses of Indian forests to climate change are mainly unknown, necessitating studies that combine phenology, climate and biotic interactions. Finally, for India, we recommend establishing a phenology network that facilitates the effective integration of phenology data collected through multiple monitoring methods, thereby strengthening phenological studies shortly.

Keywords: abiotic factors; biotic factors; climate change; reproductive phenology; vegetative phenology

Introduction

In recent decades, knowledge of plant phenology has gained significant prominence due to its potential to assess the effects of climate change on ecosystems (1, 2). Several researchers have noted that the periodicity of plant phenological events is influenced by abiotic factors, such as temperature, rainfall, humidity, soil moisture and photoperiod (3-10). The major biotic factors that have received attention in this regard are herbivores, pollinators and seed dispersers (11-16). Plant phenology has responded to climate change with shifts in timing (17, 18). The shift in plant phenology due to climate change may affect species range limits, disrupt ecological interactions at different scales and trophic levels, lead to species extinctions and thereby cause biodiversity loss (19-23). Thus, there is a need for studies that enhance our understanding of the complexity of climate-phenology interactions (24). Plant phenology has been recorded using various methods, including visual observation, satellite remote sensing and near-surface remote sensing (25-30). Emerging techniques enable researchers to integrate data across spatial and temporal scales, as well as across multiple species or ecological communities (31). India is located north of the equator, between 66°E and 98°E longitude and 8°N and 36°N latitude. As stated by ISFR, the total forest cover of the country was 713789 km², which is 21.71% of the country's geographical area. India represents significant geological, geomorphological,

climatic, biotic and cultural diversity (32). The great diversity of climatic features (tropical to arctic) and habitats (plains, wetlands and mountains) has led to a massive range of flora and fauna, which form distinct ecosystems (33). India ranked seventh among countries most affected by extreme climate change events (34). It was found that climate change is negatively affecting natural ecosystems, including the Indian forest ecosystem, with notable impacts observed in plant phenology (35, 36). Therefore, studying phenology across different forest types is crucial under changing climatic conditions. However, studies on plant phenology are still scattered in Indian forests. This paper aims to collate existing information on vegetative and reproductive phenological patterns and their influencing factors (both abiotic and biotic) across the major forest types of India, identify knowledge gaps and propose a way forward.

Methodology

Our search covered articles on plant phenology (vegetative and reproductive). To locate these studies, we conducted searches using online platforms, including Google Scholar, ResearchGate and Sci-Hub. To narrow down our search, we used the following keywords: "plant phenology in Indian forests" and "vegetative and reproductive phenology in Indian forests". More specifically, we limited our review to community-level phenological studies

conducted through visual observations within defined forest types. To examine the distribution of phenological data across major forest types, we followed Champion and Seth's forest type classification (37). Additionally, we discussed studies that employed alternative vegetation monitoring methods, including satellite-based remote sensing and near-surface remote sensing (phenocams).

In the following sections, firstly, we described the phenological patterns for each forest type based on the season in which peak vegetative (leaf initiation and leaf senescence; or growth initiation) and reproductive (flowering and fruiting) events occur unless otherwise noted. Patterns were explained based on tree phenology unless we mentioned other life forms. Since proper definitions were not given for terms such as leaf initiation, leaf flush, leaf emergence, production of young leaves and leaf bud busting and they were used interchangeably by the authors, we considered all these equivalent and hereinafter referred to them as "leaf initiation". Similarly, the terms leaf senescence, leaf fall, leaf drop, abscission of leaves and leaf shedding were collectively referred to as "leaf senescence" hereafter. Then, we explained the factors influencing phenological patterns for each forest type. We found that many studies mentioned the influencing factors but provided inadequate information. However, these factors were incorporated into the text and only studies that tested at least one variable were quantified. Finally, we concluded with recommendations for future directions in plant phenology research, emphasizing the importance of long-term and large-scale monitoring efforts.

Results and Discussions

We identified thirty-seven studies that provided community-level phenological information on plants across India's major forest types. Of these, ten studies (27.03 %) focused on moist tropical forests, eleven (29.73 %) on dry tropical forests, seven (18.92 %) on montane subtropical forests, five (13.51 %) on montane temperate forests, one (2.70 %) on subalpine forests and three (8.11 %) on alpine scrub (Table 1). In alpine and subalpine zones, phenological studies were limited to specific periods of the year, whereas in all other forest types, studies typically spanned one to three years. Four studies centred exclusively on vegetative phenology. Among the reproductive phenological studies, seven concentrated on both flowering and fruiting, while four evaluated fruiting alone. Only eleven studies included more than one life form; however, six of these, despite mentioning them in the methods, failed to differentiate phenological patterns among them. Trees were the most frequently studied life forms, with twenty-eight studies, followed by shrubs (five), herbs (three) and climbers and lianas (two each).

Moist tropical forests

In the moist forests of Uttara Kannada and in the moist deciduous forest of Similipal Biosphere Reserve, peak leaf initiation occurred during the summer season and leaf senescence took place during the winter season (38-40). Similarly, in the moist deciduous forest of the Katerniaghat Wildlife Sanctuary, leaf initiation occurred during the winter-to-summer transition and in the summer season, with maximum leaf senescence noted in the winter season (41). Leaf initiation

and leaf senescence both peaked in the early dry period in the moist forests of Kodayar (42). In the moist deciduous forest of Kanha Tiger Reserve, most species initiated leaves between the hot weather and monsoon season and the maximum incidence of leaf senescence occurred during the two dry seasons (43). The wet evergreen forest of Bhadra Wildlife Sanctuary exhibited a more complex pattern, with two distinct peaks of leaf initiation: a significant peak in the winter and a minor one in the summer and leaf senescence from rainy and winter to summer with a substantial and minor peak (44).

Most species in the moist deciduous forest of the Similipal Biosphere Reserve flowered and fruited during the summer season (40). Similarly, in the moist deciduous forest of the Katerniaghat Wildlife Sanctuary, flower bud/fig initiation was recorded during the winter-to-summer transition, as well as in the summer season and fruit formation was observed during the summer (41). In the moist forest of Uttara Kannada, trees experienced a major flowering peak in the summer season, a minor peak in the winter season and a fruiting peak in the later part of the summer season (38). The same pattern was described for shrubs and lianas of this locality; in contrast, herbs and climbers displayed major flowering and fruiting peaks during the winter period (39). In the wet evergreen forest of Bhadra Wildlife Sanctuary, flowering and fruiting took place in the dry season (44). The major flowering peak in the moist deciduous forest of the Kanha Tiger Reserve was associated with the hot weather season and fruiting peaked late in the hot weather and early monsoon (43). In the wet evergreen forest of Kalakad-Mundanthurai Tiger Sanctuary, herbs and small trees displayed peak flowering during the dry season, whereas shrubs peaked in the dry and post-monsoon seasons. Shrubs and small trees exhibited greater fruiting in the monsoon, whereas herbs fruited evenly in the dry and monsoon seasons (45). Studies on mangrove phenology from the Bhitarkanika Sanctuary and the Pichavaram mangrove forest found that most of the species started flowering in the summer season and completed fruiting in the rainy season (46, 47). However, in the moist forests of the Kodayar, two flowering peaks were recorded, a larger one during the dry period and a smaller one during the rainy season and fruiting activity was observed throughout the year (42).

In the moist forest of Uttara Kannada, leaf initiation was triggered by high temperature, minimal rainfall and increasing day length. In contrast, shorter day length and a decrease in temperature led to leaf senescence. Temperature changes likely drove flowering; additionally, flowering in various seasons may be a means to prevent pollinator competition. Fruit ripening during the summer season, especially in wind-dispersed species, could be a consequence of selection to disseminate propagules when wind velocity is maximum (38). Another study in the same forest found that the factors influencing leaf initiation and leaf senescence were similar to those in the above research. Herbs, lianas and climbers exhibited a strong negative correlation with rainfall and flowering phenology. In contrast, shrubs showed a strong positive correlation with a two-month lag in rainfall. Also, life forms did not exhibit a strong preference for fruiting phenology, except for shrubs, which had a strong negative correlation with a two-month lag in rainfall. Abundant soil moisture and hot and humid weather favoured flowering and fruiting activity. Flowering during the summer period may

Table 1. Details of phenological studies in major forest types of India (Classification based on Champion and Seth, 1968)

Major group	Location	Monitoring duration	Phenophases	Life forms	Reference
Moist tropical forests	Kanha Tiger Reserve, Madhya Pradesh	1981-1982	L, Fl, Fr	T	(43)
	Uttara Kannada, Karnataka	1983-1985	L, Fl, Fr	T	(38)
	Uttara Kannada, Karnataka	1983-1985	L, Fl, Fr	C,H,L,S	(39)
	Kalakad-Mundanthurai Tiger Sanctuary, Tamil Nadu	1991-1992	Fl, Fr	H,S,T	(45)
	Kodayar, Tamil Nadu	-	L, Fl, Fr	T	(42)
	Similipal Biosphere Reserve, Orissa	-	L, Fl, Fr	T	(40)
	Bhitarkanika Sanctuary, Orissa	-	Fl, Fr	T	(46)
	Katerniaghat Wildlife Sanctuary, Uttar Pradesh	-	L, Fl, Fr	T	(41)
	Pichavaram mangrove forest, Tamil Nadu	-	Fl, Fr	T	(47)
	Bhadra Wildlife Sanctuary, Karnataka	2004-2006	L, Fl, Fr	T	(44)
Dry tropical forests	Vindhyan Plateau, Uttar Pradesh	1987-1988	L, Fl, Fr	T	(48)
	Point Calimere Wildlife Sanctuary, Tamil Nadu	1987-1988	Fr	C,S,T	(58)
	Mudumalai Wildlife Sanctuary, Tamil Nadu	1988-1990	L	T	(54)
	Mudumalai Wildlife Sanctuary, Tamil Nadu	1988-1990	Fl, Fr	T	(56)
	Hathinala forest, Uttar Pradesh	2001-2003	Fl, Fr	T	(55)
	Coromandel coast, Tamil Nadu	2003-2004	Fr	L,T	(57)
	Bala-fort Reserve Forest, Rajasthan	2001-2003	L, Fl, Fr	S, T*	(49)
	Hathinala Forest, Uttar Pradesh	2006-2008	L	T	(53)
	Tadoba National Park, Maharashtra	1996-1998	L, Fl, Fr	T	(51)
	Bhadra Wildlife Sanctuary, Karnataka	2004-2006	L, Fl, Fr	T	(50)
Montane subtropical forests	Amrabad Tiger Reserve, Telangana	2018-2020	L, Fl, Fr	T	(52)
	Lailad, Meghalaya	1979-1980	L, Fl, Fr	T	(63)
	Lailad, Meghalaya	1982-1983	L, Fl, Fr	S	(64)
	Hills of Kangchup, Manipur	1993-1994	L, Fl, Fr	T	(61)
	Girnar Reserve Forest, Gujarat	2008-2009	L, Fl, Fr	T	(59)
	Girnar Reserve Forest, Gujarat	2008-2011	Fl, Fr	H, S	(65)
	Jaintia Hills, Meghalaya	2013-2014	L, Fl, Fr	T	(62)
	Reiek Community Reserve Forest, Mizoram	2016-2018	L	T	(60)
	Garhwal Himalaya, Uttarakhand	1986-1987	L, Fl, Fr	S, T*	(67)
	Longwood, Thaishola-Carrington and Upper Bhavani, Tamil Nadu	2000-2003	L	T	(66)
Montane temperate forests	Korakundah Reserve Forest, Tamil Nadu	2002-2004	Fl, Fr	L, S, T*	(68)
	Kukkal Reserve forest, Tamil Nadu	2002-2004	Fr	T	(69)
Subalpine forests	Eppanadu and Longwood, Tamil Nadu	2009-2010	Fr	T	(70)
	Pindari, Uttarakhand	1988-1989	L, Fl, Fr	T	(71)
Alpine scrub	Rudranath bughiyal, Uttarakhand	1984-1985	Ig, Fl, Fr	F,G,S*	(72)
	Pindari valley, Uttarakhand	1987-1988	Ig, Fl, Fr	F,G,P,S*	(73)
	Tungnath, Uttarakhand	1988-1998	Ig, Fl, Fr	F,G,S*	(74)

*, studies in which phenological pattern is not differentiated among life forms

Phenophases: L-leaf, Ig-growth initiation, Fl-flower, Fr-fruit; Life forms: C-climbers, F-cushion & spreading/tall/medium/short/forbs, G-grasses /sedges/other monocots, H-herbs, L-lianas, P-pteridophytes, S-undershrubs/shrubs, T-small trees/trees

enhance flower visibility to pollinators, as many species were without leaves. The study also found that the species that relied on dominant dispersal agents (like animals) and pollinating agents (like insects) had a significant peak of fruiting or flowering during the summer season and a smaller peak at the end of the rainy season; in contrast, passive and wind-dispersed species had a fruiting peak in the winter season (39). In the moist forests of Kodayar, leaf initiation and leaf senescence were regulated by the same variables as found in the moist forests of Uttara Kannada. A significant negative correlation was observed between flowering and rainfall. A significant positive correlation was also found between fruit ripening in animal-dispersed species and rainfall, suggesting it helps maintain moisture within the fruits. In contrast, wind-dispersed and explosively dispersed fruiting guilds had no significant correlation with rainfall, aligning with the advantages of dry spells and increased wind flow during the early summer (42). In the moist deciduous forest of Katerniaghat Wildlife Sanctuary, leaves appeared in response to the increasing daylight duration and average minimum and maximum temperature (41). In the moist deciduous forest of Similipal Biosphere Reserve, leaf senescence had a significant negative correlation with rainfall. A temperature rise favoured the development of fruits in the majority of the species. Variations in day length and temperature had driven leaf initiation, leaf senescence and flowering. Soil moisture availability may have regulated the phenological patterns of species (40). In the wet evergreen forest of Kalakad-Mundanthurai Tiger Sanctuary, rainfall had a significant negative correlation with flowering, while no significant correlation was noticed with fruiting (45). In the wet evergreen forest of Bhadra Wildlife Sanctuary, leaf senescence was likely driven by moisture stress. Rainfall had a significantly negative influence on the vegetative and reproductive phenologies. Additionally, abiotically dispersed fruits were abundant in the dry season, while animal-dispersed fruits matured at the beginning of the rainy season (44).

Dry tropical forests

Peak leaf initiation during the summer season and peak leaf senescence in the winter season were described for the seasonally dry forest of the Vindhyan Plateau, the dry deciduous forests of the Bala-fort Reserve Forest and the dry deciduous forest of the Bhadra Wildlife Sanctuary (48-50). These patterns aligned with those reported for certain moist forests. However, in other dry deciduous forests, leaf initiation occurred during the summer season and leaf senescence began in the winter and extended up to the summer season in the Tadoba National Park; in the Amrabad Tiger Reserve, leaf initiation was completed before the beginning of rain and leaf senescence reached its peak before the arrival of the intense dry period; in the Hathinala Forest, leaf initiation in most of the species occurred in the summer period and the onset of leaf senescence emerged at various times after the end of the rainy season; and dry season leaf initiation was observed in the Mudumalai Wildlife Sanctuary (51-54).

Flowering and fruiting patterns were more variable across various dry deciduous forest types. The majority of species in the Hathinala Forest flowered primarily during the summer season and all flowering types finished the fruiting phenophase in the late dry season before the start of the

subsequent rainy season (55). Flowering peaks in the Bhadra Wildlife Sanctuary occurred during the summer season and fruiting patterns happened from the rainy season to the winter season (50). In the Bala-fort Reserve Forest, flowering showed two distinct peaks: an extensive one during the summer season and another in the rainy season, with the peak fruiting in the rainy and winter seasons (49). The majority of the species in the Amrabad Tiger Reserve produced flowers during the summer season and two fruiting peaks were observed, one during the rainy season and the other during the summer season (52). In the Tadoba National Park, most species initiated flowering in late winter, which continued through summer or even into the rainy season and fruiting was observed throughout the year (51). The two study sites in the Mudumalai Wildlife Sanctuary showed remarkable differences in flowering phenology. At the wetter site, a flowering peak occurred in the late dry season, whereas at the drier site, it took place in the wet season. At both sites, peak fruiting was concentrated in the late wet season and extended into the early dry season (56). The seasonally dry forest of the Vindhyan Plateau exhibited a complex pattern, with a major flowering peak in the summer season, two secondary peaks in the winter season and the rainy season and fruit initiation during the transition from winter to summer (48). In the dry evergreen forest of the Coromandel coast, lianas experienced two fruiting peaks: a major one in the late summer season and a minor one in the rainy season, whereas trees had a single fruiting peak in the late summer season (57). Shrubs and climbers in the dry evergreen forest of Point Calimere Wildlife Sanctuary had their fruiting peak during the post-monsoon. In contrast, tree species had minimal month-wise variation in both years (58).

In the seasonally dry forest of the Vindhyan Plateau, rising temperature seemed to trigger leaf initiation, whereas low temperature initiated leaf senescence. Flowering during leafless and low-foliage periods facilitates both wind pollination and flower display to attract pollinators. Animal pollination was found to be the primary mode of pollination. Community-level flowering for a longer period ensures a sustained flow of floral foodstuffs to various groups of pollinators whose populations may peak at different times of the year (48). In the dry deciduous forest of Mudumalai Wildlife Sanctuary, a positive correlation was observed between insect abundance and rainfall progression but no correlation between rainfall and leaf initiation. Trees that initiated leaves early or synchronously during the dry period experienced significantly lower insect damage compared to those with later initiation. Furthermore, species with physical defences, like wax on their leaves, were less vulnerable to herbivore damage than those lacking such adaptations (54). In the dry deciduous forest of Hathinala, largely synchronous leaf initiation during the hot-dry summer or early rainy season indicates the combined influence of increasing day length and temperature; in contrast, leaf initiation after the first significant rainfall of the season signifies the important role of rains in this process. Leaf initiation during the dry season may serve as a strategy to minimize insect herbivore attacks. Furthermore, leaf initiation and the start of leaf senescence may be connected to varying adaptations of tree species in seasonal moisture availability (53). Research indicates that in the dry deciduous forests of Bala-fort Reserve, species exhibiting delayed leaf initiation in response to drought confirmed the influence of rainfall; in contrast, delayed flowering highlighted

the role of soil moisture. It was also found that the monsoon failure hastened the initiation of leaf senescence in some species and it was concluded that soil moisture plays a crucial role in shaping their growth period (49). The phenological patterns displayed by tropical dry forest species of Bhadra Wildlife Sanctuary appear to be connected to rainfall and temperature distribution (50). In the dry deciduous forests of Bala-fort Reserve Forest and Bhadra Wildlife Sanctuary, the synchronization of flowering and leaf initiation appears to be connected to moisture, temperature and day length (49, 50). Research indicates that in the dry deciduous forest of Hathinala, erratic precipitation and increasing temperature could alter the length of the growing season by affecting the timing of both leaf initiation and leaf senescence, with varying effects across different functional types. A rainy spell during the dry season or a drought in the rainy season may cause a change in the timing of leaf initiation and/or flowering. Five flowering types were recognized based on flowering time, potential flowering signals and the state of leaf phenology during the flowering period. Summer flowering occurred on foliated shoots during the hot-dry period; a rise in day length or temperature may serve as a flowering signal. Rainy flowering developed on foliated shoots during the warm-wet period; the first significant rains may function as a flowering signal. Autumn flowering took place on shoots with mature leaves during the period of decreasing day length. Winter flowering occurred on foliated shoots with synchronous leaf senescence and leaf initiation during the cool, dry season; leaf senescence may act as a flowering signal and dry-season flowering happened on leafless twigs during the cool, dry season soon after leaf senescence or after occasional winter rains (55). In the dry deciduous forest of Amrabad Tiger Reserve, leaf initiation exhibited a significant negative relationship with three-month lag rainfall and leaf senescence showed a significant negative relationship with both current rainfall and one-month lag rainfall. A significant positive relationship was verified between flowering and rainfall with a three-month lag, whereas fruiting was significantly positively related to rainfall with a one-month lag. Insect pollination was more common and the majority of the species were dispersed by wind in the dry season (52). Research indicates that at the wetter site of the dry deciduous forest of Mudumalai Wildlife Sanctuary, flowering exhibited the highest time-lag correlation with rainfall during a two-month lag period. However, at the drier site, the frequency of flowering was positively correlated with rainfall during the corresponding month. The study identified distinct flowering patterns linked to pollination guilds: bird-pollinated guilds flowered only during the dry season, possibly to enhance the visibility of their large flowers to pollinators when trees were leafless; insect-pollinated guilds exhibited no clear seasonality in flowering at the wetter site, but flowering during the dry months at the drier site appeared constrained by moisture availability; and wind-pollinated guilds flowered primarily during the wet season when wind speeds were highest and beneficial for pollen movement. Staggered flowering exhibited by wind-pollinated species could be related to the avoidance of heterospecific pollen transfer. Fruiting occurred after rainfall, with a lag of approximately two months. Many species had different vectors for pollination and dispersal, implying that dependence on a single vector for both pollination and seed dispersal may impose constraints on pollen and fruit or seed dispersal. Animal-

dispersed species peaked during the wet seasons, while explosively dispersed fruits dehisced in the dry months when relative humidity was low. Additionally, wind-dispersed species showed no clear correlation with wind speed (56). In the dry deciduous forest of Tadoba National Park, species producing fruits and seeds in the late winter or early summer were wind- or animal-dispersed (51). Research indicates that in the dry deciduous forest of the Coromandel coast, maximum fruiting frequency showed a positive correlation with the highest temperatures. At the same time, rainfall influenced fruiting in certain species. Wind-dispersed species attained their fruiting peak during the driest months, suggesting that dryness facilitates seed dispersal; fruiting in animal-dispersed species was also found to peak during the dry season (57). In the dry evergreen forest of Point Calimere Wildlife Sanctuary, abiotic variables, particularly temperature, had a greater impact on the timing of fruiting than biotic variables (58).

Montane subtropical forests

In the mixed subtropical deciduous forest of Girnar Reserve Forest, the highest leaf initiation took place in the summer season and peak leaf senescence was noticed during the winter season (59). In the moist subtropical hill forest of Reiek Community Reserve, the leaf initiation peaked during the cool winter to dry summer and leaf senescence peaked during the cool, dry period (60). In the subtropical mixed forests of the hills of Kangchup, two peak periods of leaf initiation were distinguished: the first peak in the summer season and the second peak in the rainy season and peak leaf senescence was noticed during the winter season (61). Peak leaf initiation was observed during the rainy season in the subtropical broadleaved humid forest of Jaintia Hills and peak leaf senescence was concentrated during the winter and spring (62). In the subtropical humid forest of the Lailad, trees attained peak leaf initiation at the end of the dry season and the beginning of the monsoon; in contrast, shrubs in this locality initiated leafing in the dry season. The leaf senescence of most of the tree species and shrub species coincided with the dry season (63, 64).

Trees in the subtropical humid forest of Lailad predominantly flowered and fruited during the wet season; in contrast, shrubs in this locality exhibited maximum flowering in the summer season and fruiting in the monsoon season (63, 64). In the mixed subtropical deciduous forest of Girnar Reserve Forest, the trees exhibited major flowering during the winter season and fruiting occurred during the winter-to-summer transition, as well as in the summer season; in contrast, herbs, shrubs and undershrubs in this reserve displayed peak flowering in the monsoon season and fruiting in the winter season (59, 65). In the subtropical mixed forests of the hills of Kangchup, two flowering peaks were noted: a major one in the warm, dry season and a minor one in the rainy season and the fruiting happened in the cool and dry winter (61). Two flowering peaks were also observed in the subtropical broadleaved humid forest of Jaintia Hills in spring and autumn and a fruiting peak was concentrated in the autumn season (62).

Research indicates that flowering and leaf initiation in the subtropical mixed forests of the Kangchup hills are synchronized and may be influenced by moisture, temperature and photoperiod (61). Similar patterns were also reported in a few dry deciduous forests. In the subtropical broadleaved humid

forest of the Jaintia Hills, leaf initiation occurred with the onset of rain. Pollination was predominantly carried out by the insects (62). Photoperiod and minimum temperature had the strongest correlation with the phenological activity in the moist subtropical hill forest of the Reiek Community Reserve (60). Research indicates that in the subtropical humid forest of Lailad, a large number of species exhibited maximum leaf initiation in the warmer months of the year before the rains; in contrast, leaf initiation in various species terminated with a fall in temperature and decrease in day length. Blooming periods of congeneric species did not coexist substantially, an adaptive strategy to avoid competition for common pollen vectors. The study also found that fruits produced during the dry season were mainly dry and the majority of the dry season fruiters, like some extended fruiters, typically produce small, winged seeds whose dispersal was promoted by wind currents; in contrast, most of the species developed fleshy fruits during the wet season (63). In the mixed subtropical deciduous forest of the Girnar Reserve Forest, temperature and wind speed showed no positive significance with flowering and fruiting and rainfall did not affect phenology directly (65).

Montane temperate forests

In the Longwood, Thaishola-Carrington and Upper Bhavani sites and in the Garhwal Himalaya, peak leaf initiation occurred during the dry season and leaf senescence in the winter season (66, 67). All studies conducted in these forests revealed a consistent reproductive pattern: peak flowering occurred during the summer season and fruiting reached its peak during the rainy season in the Garhwal Himalaya and Korakundah Reserve Forest (67, 68). A similar fruiting peak during the rainy season was also observed in the Kukkal and Longwood and Eppanadu sites (69, 70).

Research indicates that in the Longwood, Thaishola-Carrington sites and Upper Bhavani sites, rainfall, the number of rainy days and soil moisture exhibited significant adverse effects on leaf initiation phenology. At the same time, sunshine had a positive impact during the one-month lag period at the Longwood site. The study also found that leaf senescence was negatively influenced by soil moisture during the corresponding month at the Thaishola-Carrington and the Longwood sites, whereas at the Upper Bhavani site, maximum temperature had a significant negative influence during the corresponding month and one-month lag period (66). In Garhwal Himalaya, individuals inhabiting the eastern slopes showed earlier flowering and fruiting than those on the northern slopes, which was ascribed to the temperature effect (67). Research indicates that in the Korakundah Reserve Forest, flowering was governed by temperature and fruiting by rainfall. Photoperiod, or sun-related factors, may be the most reliable cue for flowering. Additionally, flowering during the dry season attracts numerous pollinators, thereby improving fertilization potential and promoting coexistence among different pollinator species. Bees, birds and diverse insect pollination guilds were active during the dry season. Explosive and wind dispersal occurred during the dry/wet season, whereas animal dispersal was significantly higher in the wet seasons (68). In the Kukkal Reserve Forest, research indicates that total monthly rainfall and the number of rainy days exhibited a significant positive correlation with total fruit production; in contrast, the number of fruiting species showed a

significant positive correlation with humidity and the monthly mean maximum and minimum temperatures (69). In the Eppanadu and Longwood sites, the highest fruiting activity during the monsoon may be an adaptation to utilize the moisture content for fruit maturation (70).

Subalpine forests

A study from Pindari revealed that leaf initiation happened in the summer period and leaf senescence culminated with the advent of winter. The maximum population of species was recorded in flowers during summer and in most species, the appearance of fruits took place in the rainy season. In Pindari, as summer approaches, the increased temperature causes the snow to melt quickly, which serves as a strong signal to end the long winter dormancy of both vegetative and flower buds. Leaf senescence activity appeared to be positively related to decreasing atmospheric temperature. Most species were adapted well for wind pollination and wind dispersal. The delayed maturation and prolonged retention period of fruits further increase their potential for wind dissemination in the early winter months when strong, dry winds blow in the area before snowfall (71).

Alpine scrub

Studies in the alpine zone have consistently exhibited a phenological pattern. In the majority of species observed in Rudranath bughiyal, Pindari valley and Tungnath, growth was initiated before the onset of the monsoon and senescence was attained gradually during the monsoon season. Notably, the majority of alpine plants flowered and fruited during the monsoon season. In the studies mentioned above, early growth initiation was attributed to the rise in temperature, the onset of snowmelt and the early availability of soil moisture (72-74). In the Pindari valley, vegetative growth, flowering and fruiting seemed to be directly governed by absolute or relative soil temperature. Additionally, the flowering time of the species occurring at various locations also differed, perhaps due to photoperiodic responses (73). Variations in photoperiodic and thermoperiodic responses among species caused differences in flowering times in Tungnath (74).

Current Progress and Future Perspectives

Visual observations of plant phenological stages have been made for over a century in various locations. Several observation networks or citizen science initiatives have been initiated around the world, like the USA National Phenology Network (<http://www.usanpn.org/>), Phenobs (<https://www.idiv.de/en/phenobs>), the ITEX network (<https://www.gvsu.edu/itex/>), Nature's Calendar (UK: <http://www.naturescalendar.org.uk/>), Plant Watch (Canada: <http://www.naturewatch.ca/plantwatch/>), Natuurkalender (Netherlands: <http://www.natuurkalender.nl/>) and Climate Watch (Australia: <https://www.climatewatch.org.au>), to provide support for long-term phenological databases. In India, we found a citizen project dedicated to tracking seasonal phenology, SeasonWatch (<http://www.seasonwatch.in>), which began in 2010. Its ultimate goal is to comprehend geographical variations and the effects of climate change on the phenology of widely distributed tree species. In addition to formal literature (floras, scientific articles, tree guides, etc.), there is also anecdotal and cultural knowledge about expected phenological patterns; however, this project

encounters several challenges, involving the need for sufficient sample sizes per species per season from different locations as well as concerns regarding data quality and accuracy (75).

According to our revision, the above-mentioned phenological studies used a wide range of definitions and methods for data collection, which can hamper analysis across studies. Globally, experts have developed standardized protocols for phenological observations. One such protocol, established by the USA National Phenology Network, encompasses taxonomic groups and ecosystem types for terrestrial, freshwater and marine plant and animal taxa. It contains elements that enable improved detection and description of phenological responses, together with the assessment of phenological "status" or the capacity to track the presence-absence of a particular phenophase, as well as standards for recording the degree to which phenological activity is denoted in terms of intensity or abundance (76). Similarly, the Phenobs protocol (<https://www.idiv.de/en/phenobs/protocols-data-policy.html>) has been established by the Phenobs project for monitoring phenological stages and intensity for herbaceous plant species in botanical gardens across a global range of sites. Furthermore, it covers the measurement of plant traits and documentation of temperature and precipitation in all participating gardens. Another protocol is the ITEX species protocol, which the ITEX network has generated to examine the diversity and traits of vascular plants in the species pools of arctic and alpine tundra areas. Here, the response variables are classified into two primary groups: phenological (P) and quantitative (Q), both of which encompass both vegetative and reproductive traits. In connection with this program, climate data such as air temperature, precipitation, wind velocity, global solar radiation and relative humidity are recorded from ITEX climate stations and a particular number of insect studies are also included, as specified in the chapters of the ITEX Manual (<https://www.gvsu.edu/itex/library-8.htm>). Additionally, the herbivory network is operational and the outlined protocol (<https://herbivory.lbhi.is/protocols/>) provides guidelines for the assessment of herbivory occurrence and intensity within ITEX plots and among study sites. We have noticed that the above protocols have given less importance to factors influencing phenology, except for the ITEX species protocol. However, India currently lacks similar phenology networks and standardized protocols. To advance phenological studies shortly, it is essential to establish a systematic, long-term monitoring network through collaboration among academic institutions, governmental and non-governmental agencies and citizen science initiatives.

Circular statistics have been identified as the most commonly used tool for analyzing plant phenology globally (26, 77–79), as they apply well to plant phenological research, from the generation of so-called phenological variables to testing hypotheses of random versus non-random seasonal patterns (80). However, only three of the above-mentioned studies (44, 50, 66) applied circular statistics to phenological datasets, while the remaining studies simply represented the peak seasons and months of different phenophases without providing a quantitative analysis of seasonality, which may limit our ability to investigate and better interpret phenological patterns. Relatively few studies (fifteen out of thirty-seven studies) had explicitly explored the correlation between phenology and abiotic factors, considering rainfall (39, 40, 42, 44, 45, 50, 52, 54, 56, 57, 60, 65, 66, 68, 69), temperature (40, 42, 50, 57, 60, 65, 66, 68, 69), wind (56, 65),

moisture (39, 66), humidity (69), sunshine (66) and photoperiod (60). To understand long-term drying, the loss of minimum temperature cues and other slow-occurring climate impacts, future studies should utilize long-term phenology data and meteorological data (24). Variations in phenology patterns are unlikely to be fully explained by a single environmental driver, as multiple factors influence phenological responses under climate change (81). We found only seven studies (39, 42, 48, 54, 56, 57, 68) that aimed to determine the biotic factors influencing phenology. These studies primarily focused on pollination and/or seed dispersal, either classifying species based on their pollination and seed dispersal modes and/or examining the seasonal specificity in species with various pollination and dispersal modes. However, we could only find a single study that attempted to understand the effect of herbivory on leaf phenology (54). Thus, there is a huge gap in our understanding of factors involved in phenology. However, international studies stand out in this respect; one study looked at the environmental and biotic constraints on the reproductive phenology of a northeast Brazilian mangrove community (82). Another relevant study in the tropical savanna identified that environmental factors influence the phenological events of anemochoric plants and increase the potential for diaspore dissemination (83). Climate change is altering the cues and drivers that regulate phenology in tropical forests (84). The timing of vegetative phenophases is crucial for herbivores; similarly, reproductive phases tend to be adjusted to match the accessibility and phenology of mutualists, such as pollinators and seed dispersers. However, with rapid changes in climate, these leaf-herbivore, flower-pollinator and fruit-disperser interactions may become decoupled from their evolutionarily synchronized phenophases (85) and therefore have broader impacts on the forest community. Hence, research linking climate, phenology and trophic interactions is necessary. These data are crucial for planning conservation and management strategies and will improve our capacity to identify and predict the cascading effects of climate change on forest ecosystems (24).

Although visual observations enable researchers to examine plant life cycles closely, these studies are often limited to short periods and localized areas. Satellite remote sensing offers an alternative approach for studying vegetation phenology, allowing for observations over progressively longer periods and at larger scales (86). In India, phenological studies have primarily relied on visual observations, with relatively fewer studies utilizing remote sensing techniques. As shown in Table 2, four different satellite sensors, MERIS (Medium Resolution Imaging Spectrometer), SPOT-VEGETATION (Satellite Pour l'Observation de la Terre), AVHRR (Advanced Very High-Resolution Radiometer) and MODIS (Moderate Resolution Imaging Spectroradiometer), have been used for phenological studies in India. MODIS is the most frequently used sensor (four studies), followed by AVHRR (three). We found that in India, remote sensing has been used in phenology research, primarily to document leaf phenology. However, some researchers have utilized satellite remote sensing for predicting and detecting flowering phenology (96, 97). We also found that the phenological metrics and their definitions, as derived by researchers, varied from study to study. However, satellite-based remote sensing in phenological research faces larger uncertainties due to low temporal and spatial resolution, cloud cover contamination and the modifiable area unit problem

Table 2. Summary of satellite-based phenological research in India

Study site	Vegetation type	Sensor	Duration	Acquisition	Spatial Resolution	Phenology metrics	Reference
Kerala, Karnataka Meghalaya, Uttarakhand, Arunachal Pradesh, Orissa, Madhya Pradesh Jharkhand, Goa	Tropical evergreen, Subtropical evergreen, Tropical moist deciduous, Tropical dry deciduous, Tropical semi-evergreen	MERIS	2003-2007	8 day	~ 4.6 km	OG (onset of greenness), ES (end of senescence)	(87)
Karnataka	Evergreen/semi-evergreen, Secondary/moist deciduous	SPOT-VGT	1999-2007	10 day	1 km	SFS (start of foliage season), MFS (maximum of foliage season), OFS (optimal foliage/leaf senescence), EFS (end of foliage season), LFS (length of foliage season)	(88)
Northern high-latitude	Mosaic vegetation/cropland, Broadleaved deciduous forest, Needleleaved evergreen forest, Needleleaved deciduous or evergreen forest, Mixed broadleaved and needleleaved forest, Mosaic forest/shrubland	AVHRR	1982-2006	15 day	8 km	SOS (start of season) EOS (end of season)	(89)
Madhya Pradesh	Moist deciduous	MODIS	2009	8 day	1 km	Duration of leaf flush period, leafless period, period of halfway change during leaf fall and leaf flush, leaf flush rate, leaf fall rate, leaf strategy index	(90)
Sikkim	Sikkim Himalaya	AVHRR	1982-2013	15 day	8 km	SOS (length of growing season), EOS (end of growing season), LOS (length of growing season)	(91)
Assam	Moist deciduous	MODIS	2006-2015	16 day	250 m	SOS (start of season), EOS (end of season), LOS (length of season), POS (peak of season)	(92)
Central India, Gujarat Rajwara, Central Plateau, Eastern Plateau, Central Highlands, Malabar coast	Dry and moist teak forest	MODIS	2000-2013	16 day	1 km	SOS (start of season), EOS (end of season), LOS (length of season), POS (peak of season)	(93)
Arunachal Pradesh	Alpine treeline ecotone, Arunachal Pradesh Himalaya	AVHRR	1982-2014	15 day	8 km	SOS (start of the growing season)	(94)
Maharashtra, Madhya Pradesh, Chhattisgarh, Odisha, Jharkhand	Moist deciduous, Dry deciduous, Evergreen, Semi-evergreen	MODIS	2001-2018	16 day	250 m	AD (annual deciduousness), RAD (relative annual deciduousness)	(95)

(MAUP). Additionally, ground observations record specific phenological events at the individual species level, which makes it difficult to analyze with satellite data at the regional scale due to footprint mismatch (98).

More recently, near-surface remote sensing methods, such as phenocams, have become valuable for bridging the gap between satellite-based monitoring and traditional ground observations (99, 100). The phenocam system tracks vegetation phenology at both individual and local area levels with high spatial and temporal resolution, using images from digital cameras mounted on towers. This system captures images in red, green and blue (RGB) and, optionally, in infrared (IR) bands. The generated data from phenocam imagery have been utilized for phenology studies (98). A global PhenoCam Network is emerging with regional networks, including the PhenoCam Network in the United States (<http://phenocam.sr.unh.edu>), EuroPhen in Europe (<http://european-webcam-network.net>), PEN (Phenological Eyes Network) in Japan (<http://pen.agbi.tsukuba.ac.jp>), the e-Phenology Network in Brazil (<http://www.recod.ic.unicamp.br/ephenology>) and the APN (Australian PhenoCam Network) in Australia (<http://phenocam.org.au/>). These networks can assess the effects of global change on plant phenology, production and function over timescales spanning from seasons to decades (100). In India, under the ISRO–Geosphere Biosphere Programme, a study utilized digital cameras for phenological monitoring and compared their results with satellite-based data. However, the study's duration was less than a year (101). At present, a collaborative study (2021–2024) is also underway under the ISRO–Geosphere Biosphere Programme, focusing on the Indian forest ecosystem. This study explores the techniques for retrieving phenological parameters from remote sensing data through model calibration and product validation using the proposed PhenoCam Network. In this study, Planet-Dove, IRS-AWiFS, OCM2-NDVI, SPOT-VGT&PROBA-V, MODIS, INSAT-3A-CCD NDVI, SCATSAT-1 and NOAA-AVHRR-NDVI, with weekly to decadal temporal resolution and 3 m–8 km spatial resolution, have been utilized to deduce phenological parameters such as start of the season (SOS), end of the season (EOS) and length of the season (LOS) (<https://www.isro.gov.in/>).

Conclusion

Phenological research in Indian forests was fragmentary, with significant gaps in both spatial coverage and exploration of biotic factors. However, some progress was made in identifying phenology patterns and abiotic drivers. For a better understanding of the impacts of climate change on plant phenology, future research should address phenology in the context of climate and biotic interactions; such insights are also vital for conservation and management in vulnerable forest ecosystems. In India, long-term phenological data were rare, with only a few studies utilizing satellite remote sensing approaches. Gaining insight into the causes and consequences of phenological variations requires the establishment of long-term monitoring networks with standardized protocols. Such efforts can be advanced through increased collaboration among academic institutions, governmental and non-governmental organizations and citizen science initiatives. Furthermore, the effective integration of phenological data collected through

multiple monitoring methods is required to bridge the existing knowledge gaps and it will also facilitate answering critical questions about global climate change.

Acknowledgements

The authors sincerely thank the KSCSTE-Kerala Forest Research Institute for providing the necessary facilities that enabled them to complete this work successfully. The authors gratefully acknowledge the Kerala State Council for Science, Technology and Environment for providing a research fellowship to VMT for her PhD.

Authors' contributions

All authors contributed to the conception and design of the study. VMT prepared the first draft of the manuscript. VBS and KAS provided critical revisions, intellectual inputs and overall supervision. The final version of the manuscript has been read and approved by all the authors.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

Ethical issues: None

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Peer review: Publisher thanks Sectional Editor and the other anonymous reviewers for their contribution to the peer review of this work.

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Publisher information: Plant Science Today is published by HORIZON e-Publishing Group with support from Empirion Publishers Private Limited, Thiruvananthapuram, India.