Chapter 11
Mesic Temperate Deciduous Forest Phenology

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Abstract Temperate deciduous forests are distinguished from other deciduous forests around the world by their predictably regular seasonality between dormant and active seasons. This seasonality is characterized by dramatic changes in canopy structure and function, and even overall ecosystem activity. Driven primarily by climatological temperature patterns, these cycles of vegetative development and senescence give rise to seasonal changes in biogeochemical cycling and ecological processes. Trophic and ecological interactions are regulated by phenological patterns, influencing competition and ecosystem energy flow. Phenology-mediated fluxes of water, energy, and carbon feed back into the climate system and can influence microclimate as well as local-to-regional weather and larger-scale circulation patterns. In recent decades, temperate deciduous forest phenology has shown a strong sensitivity to climate variability and change, leading to a heightened interest in phenological research in the Anthropocene. In the past decade, we have learned much about the mechanisms and drivers of deciduous forest phenology, and how it might react to future climatic changes. These insights have been obtained through observational, experimental, and modeling efforts. Here, we review what is currently understood about the biological and environmental drivers of temperate deciduous forest phenology. We discuss biosphere-atmosphere feedbacks, modeling strategies, and climate change impacts in the context of the phenology of mesic temperate deciduous forests. We highlight specific areas of uncertainty where more research is still required.

11.1 Introduction

Phenological observations on temperate deciduous trees, particularly spring flowering dates of cherries and other showy fruit trees, have been recorded for millennia (Aono and Kazui 2008; Liang 2019), with the first empirical phenological research studies dating back about two centuries (Morren 1853). Historically, the timing of phenological events provided important cues for planting and harvesting, hunting, and fishing. For example, Maine folklore holds that the best time for spring trout fishing is when the leaves on the alder (*Alnus* sp.) are the size of a mouse's ear. While there was some academic research on deciduous tree phenology during the early and mid-twentieth century (Phillips 1922; Holttum 1940; Huberman 1941), the number of publications each year was small even through the 1980s (Tang et al. 2016). However, in recent decades the development of new technologies, observation methods, and research approaches—not to mention the relevance of phenology in the context of global change biology—has brought about a heightened interest in phenological research in temperate deciduous forests (Zhang et al. 2003; Richardson et al. 2009; Gonsamo et al. 2012; Tang et al. 2016; see Fig. 11.1 for a timeline of key events in the history of phenological study).

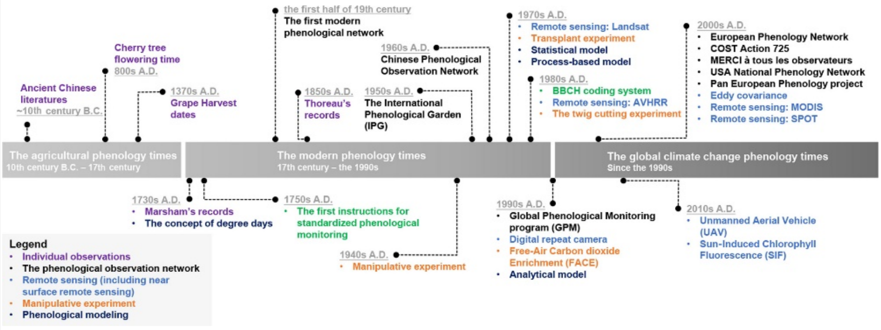

Fig. áá.á Timeline illustrating key events, technological developments, and advances in experiments and modeling, as related to the evolution of the field of phenology. Many of these milestones have been accomplished in the context of research on mesic temperate deciduous forests. Source: Piao et al. ĮąóáįÓ.

In temperate deciduous forest ecosystems, the seasonal rhythms that define the start, end, and overall length of the growing season are variable from year-to-year. Leaf developmental cycles are sensitive to the timing and magnitude of several climatic variables, most importantly maximum and minimum temperatures. Though much has been uncovered about these sensitivities, there are still several knowledge gaps about the drivers and mechanisms of phenological changes, and how interactions among these drivers under novel climate scenarios will influence future phenological shifts. Gaining a better understanding of these drivers and underlying mechanisms is necessary for management – conservation, forestry, horticulture and pomology, watershed hydrology, and carbon (C) sequestration – as well as ecological applications (biogeochemical cycling, plant productivity, and biophysical feedbacks), and mitigation of climate change impacts (Chuine and Beaubien 2001; Desai 2010; Keenan et al. 2012; Richardson et al. 2013; Ettinger et al. 2022).

Mesic temperate deciduous forests, which cover 6% of the Earth's land area (Saugier et al. 2001), alone hold ~10% (~400 Pg C) of all land carbon (Bonan 2008). These ecosystems can sequester large amounts of carbon each year (on an area basis, up to roughly 300 g C m^{-2} $year^{-1}$; Bonan 2008). The fate of carbon stored in these forest ecosystems depends on sustained forest health and productivity, which is at least partially linked to future shifts in phenology and hence growing season length (Keenan et al. 2012).

In this chapter, we focus on (1) the current understanding of the drivers of vegetative phenological transitions into and out of dormancy in mesic temperate deciduous forests, with a discussion of future research directions for both spring and fall phenology, (2) current modeling strategies and opportunities for improvement, and (3) impacts on ecosystem processes. However, there are many important aspects of mesic temperate deciduous forest phenology outside the scope of this chapter. For more information about those topics, we direct the reader to the references cited.

- Living collections phenology, e.g., in arboreta or public gardens: Gallinat et al. 2018; Primack et al. 2021; Fitzpatrick et al. 2022.
- Migration and shifting species distribution: Gauzere et al. 2020.
- Root phenology: Abramoff and Finzi 2015; Radville et al. 2016; Sloan et al. 2016.
- Phenology of cambium, fruit, flowers, and their relation to leaf phenology: Perez-de-Lis et al. 2016; Wolf et al. 2017; Ettinger et al. 2018; Savage and Chuine 2021; Arend et al. 2024.
- Urban phenology: Jochner and Menzel 2015; Wohlfahrt et al. 2019; Meng et al. 2020; Meng et al. 2022; Donnelly et al. 2024.
- Phenological asynchrony: Menzel et al. 2006; Reed et al. 2013; Gallinat et al. 2015; Kharouba and Wolkovich 2020.

11.1.1 Phenological Studies: The Current Landscape

Observational phenological studies range in resolution and spatial scale from individual tree branches and crowns, to ecosystems and landscapes, to entire regions depending on the questions asked and observation technique used (Klosterman et al. 2014). These include:

- ground-based human observation (branch-to-crown, scale ≈100-101 m)
- repeat digital photography ("PhenoCams," branch-to-canopy, ≈100-102 m)
- unmanned aerial vehicles (crown-to-ecosystem, ≈101-103 m)
- eddy covariance "flux towers" (ecosystem-to-landscape, ≈102-103 m) and
- satellite platforms (crown-to-region, ≈101-105 m).

There are tradeoffs among these methods and scales, e.g., between the ability to resolve individual organisms vs. the ability to cover large areas. Similarly, there are tradeoffs between spatial and temporal resolution; often, platforms with the highest spatial coverage have the lowest temporal resolution, and platforms with the highest temporal resolution have the lowest spatial coverage.

Using these techniques at different scales to gather long-term observations has allowed for the development of phenology models whose predictions can then be validated against independent observations (Melaas et al. 2016). These validated models provide a robust basis for extrapolation and upscaling in time and space. As a result, phenological forecasts have improved in recent decades (Wheeler et al. 2024). Models generally include drivers such as the timing and intensity of warm and cold temperatures, day length, timing of other phenological events, and other é

environmental factors such as vapor pressure deficit, soil moisture, or precipitation. However, there is still much to be learned about phenological drivers, how these drivers interact with each other, the underlying physiological mechanisms, and how all the above vary among species and populations (Grabska-Szwagrzyk and Tymińska-Czabańska 2023). Some of these outstanding knowledge gaps cannot be resolved by observational studies because in nature, drivers interact and work in concert, so sometimes experimental treatments are needed to parse the true effects of individual drivers, one at a time. In addition, models tuned to current environmental conditions may not capture nonlinear responses to future changes in drivers, but experiments let us study how plants might respond to future climate extremes now.

Experiments take place in controlled environments to isolate the effects of individual drivers (e.g., daylength or temperature) on phenological processes (e.g., the SPRUCE experiment: https://mnspruce.ornl.gov/). Experiments can help disentangle the physiological mechanisms behind phenological changes (Hänninen et al. 2019). However, experiments may lack realism or practicality (Wolkovich et al. 2012; Wolkovich et al. 2022). For example, experiments that manipulate photoperiod (daylength) often do not represent real-world combinations of photoperiod and temperature. It is also difficult to conduct experiments on mature trees – or at least to apply an experimental treatment to a whole tree. Finally, experiments are often conducted on a relatively small scale and can lack the spatial, temporal, and sampling breadth of some observational studies (Wolkovich et al. 2012). Nonetheless, the combination of observational and experimental approaches has led to enhanced predictive models and a growing understanding of the dynamics of temperate deciduous forest phenology. Below, we review recent progress of the growing understanding of mesic temperate deciduous forest phenology.

11.2 Climates of Mesic Temperate Deciduous Forests

Mesic temperate deciduous forests are found in the Northern Hemisphere at latitudes 30° to 60°N in North America, Europe, and Asia. In the Southern Hemisphere, they are found at latitudes 25° to 50°S in South America and Australia (Fig. 11.2). The term 'mesic' describes this biome's abundant annual rainfall (750 to 1,500 mm/yr.) and 'temperate' characterizes its range of mild average daily temperatures (-30 to 30°C), with an annual average of 10°C. This temperature regime causes seasonal phenological responses among the biome's deciduous species. 'Deciduous,' from the Latin word *decidere* meaning 'to fall down or off,' represents the seasonal shedding of leaves among native vegetation. Common broadleaf tree genera include oak (*Quercus*), maple (*Acer*), hickory (*Carya*), and beech (*Fagus*) in the Northern Hemisphere, with southern beech (*Nothofagus*) and *Eucalyptus* being most common in the Southern Hemisphere (Adams et al. 2019). The deciduous forest understory is typically occupied by a diversity of shrubs, mosses, and forbs.

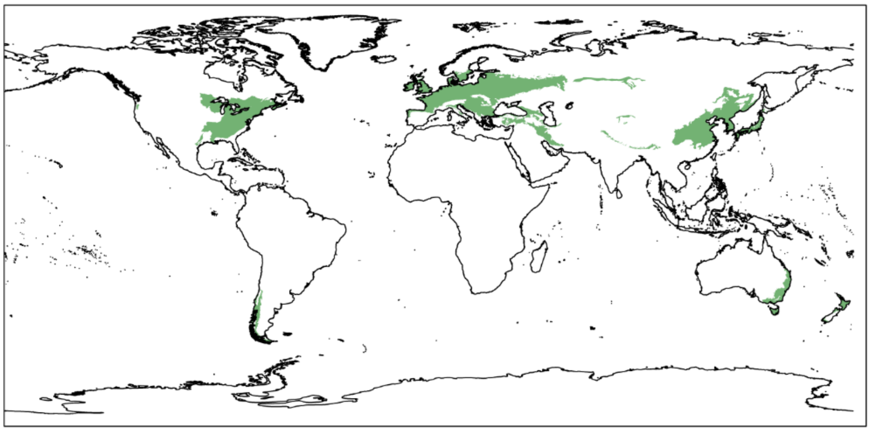

Fig. áá.ạ Geographic distribution of mesic temperate deciduous forests. Source: World Wildlife Fund and world basemap acquired from VDS Technologies.

11.3 Spring Phenology

In mesic temperate deciduous forests, the emergence of new leaves (budburst) is the first macroscopically observable spring phenophase. Depending on latitude, budburst may occur anywhere between the end of March and the end of May. However, budburst is preceded by a bud dormancy phase that staves off leaf development during winter, even if conditions might appear favorable for growth (e.g., during a brief spell of unseasonably warm weather). The dormancy phases followed by growth initiation are broken up into endodormancy and ecodormancy (see Fig. 11.3 for a schematic of dormancy progression). Across most temperate deciduous species, the release of dormancy is primarily controlled by interactions among (1) the duration and intensity of winter cold temperatures, (2) the progression of warming spring temperatures, and (3) a steadily lengthening photoperiod from the winter solstice to the summer solstice (Flynn and Wolkovich 2018).

11.3.1 Endodormancy

Endodormancy is initiated and maintained by genes that regulate levels of abscisic acid (ABA), the primary growth-inhibition hormone in bud tissues (Liu and Sherif 2019). ABA is thought to block the transport of growth-promoting hormones between plant cells as they enter and progress through dormancy (Tylewicz et al. 2018). During endodormancy, bud scales protect meristematic tissues and house premature leaves. As temperatures warm in late winter, these buds begin to swell with water. However, buds need to experience a required amount of cold weather (chilling days or chilling hours) before they transition out of endodormancy and into ecodormancy. Internal biological controls prevent these buds from breaking prematurely (Cooke et al. 2012).

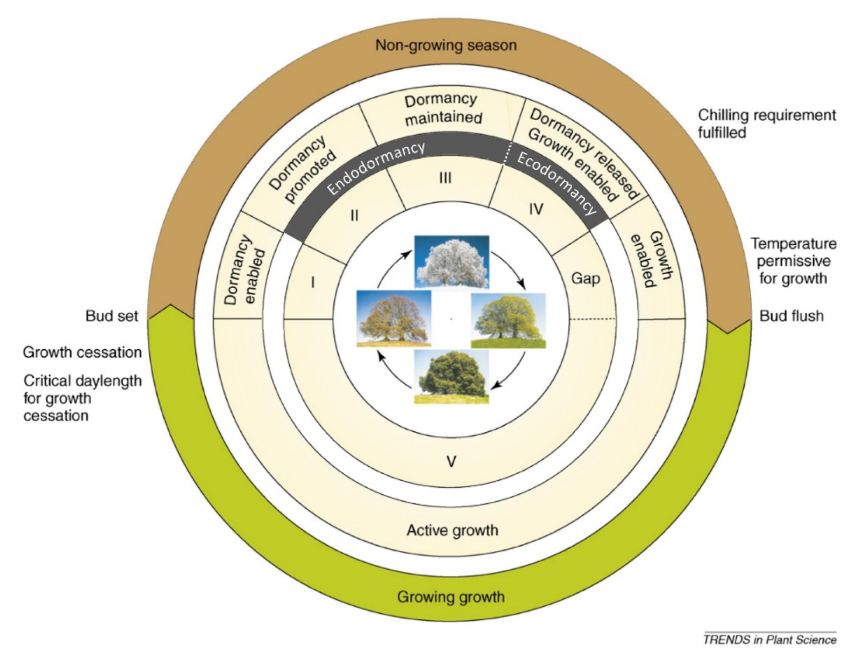

Fig. áá.ą Transitions in seasonal growth–dormancy cycling in Populus sp. Poplars synchronize the onset of the dormant period mainly with changes in day length that are sensed by phytochromes. Bud flush and bud set delimit the growing season. Prolonged exposure to chilling temperatures will release plants from dormancy. Growth resumes once the temperature passes a critical threshold. Absence of growth before and after endodormancy is caused by different environmental factors. The inner circles depict the growth–dormancy status and the corresponding meristem stages: I, cessation of cell division; II, establishment of łendońdormancy or loss of responsiveness to growthǫ promoting signals; III, maintenance of łendońdormancy; IV, release from łendońdormancy state or cell cycle machinery regaining responsiveness to growthǫ promoting signals łĮecodormancy initiationÓń; and V, resumption of cell division. 'Gap' between stage IV and V denotes the phase where growth does not occur because of purely environmental restraints. Source: figure and caption both from Rohde Í Bhalerao ąóóí; modifications to caption indicated by square brackets łń. The figure has been modified to include boxes labeled "Endodormancy" and "Ecodormancy."

The endodormancy chilling requirement acts as a 'do-not-disturb' feature, by preventing a succession of warm winter days from triggering premature leaf development. This mechanism protects new leaves from damaging frost exposure, preventing cases where premature budburst is followed by a large drop in temperature. As chilling hours accumulate throughout the winter, the activity of genes that control the synthesis and release of ABA-catabolizing enzymes steadily increases, which reduces the concentration of ABA in bud tissues. Once the chilling requirement has been met, the 'do-not-disturb' feature is turned off, triggering endodormancy release. A likely explanation for this is that ABA concentrations have reached a minimum and are no longer abundant or effective enough to exercise inhibitory effects (Rohde and Bhalerao 2007; Pan et al. 2021). The amount of chilling required for endodormancy release varies across species, and across populations in relation to regional climate (Polgar et al. 2014).

Following the initiation of endodormancy release, genes responsible for regulation of growth-promoting hormones like gibberellins (GAs) and auxins start to increase in activity. GAs promote cell division, but the functions that govern natural upregulation of GAs in buds and their physiological mechanisms in endodormancy release are not yet well-understood (Cooke et al. 2012). However, increases in GA abundance during the chilling period likely up-regulate hydrolases that break down barrier-forming callose at the plasmodesmata between cells, allowing more cell-to-cell communication (Zhang et al. 2018; Yang et al. 2021). When sufficient chilling triggers endodormancy release, buds are in a state of ecodormancy, awaiting additional environmental signals (warmth and photoperiod) to trigger bud-break (first visible leaf tips emerging from bud) and leaf-out (growth and expansion of leaves).

11.3.2 Ecodormancy

Following the induction of ecodormancy, buds must experience certain thresholds of warm weather (‘forcing’) and photoperiod for budbreak to occur. The thermal forcing requirement is species-dependent, just like the chilling requirement. Tree populations are also genetically and geographically adapted to exhibit specific chilling and forcing requirements (Cooke et al. 2012). While it is generally thought that forcing can only occur after chilling requirements have been met, some studies have suggested that forcing can occur simultaneously, or in parallel, with chilling, i.e., daily maximum temperatures can contribute to forcing requirements while at the same time daily minimum temperatures contribute to chilling (Landsberg 1974; Meng et al. 2020). Other studies have suggested that as more chilling is accumulated, forcing and photoperiod requirements are reduced (Cannell and Smith 1982; note that while this study was conducted on the conifer *Picea sitchensis*, the same concept has been applied to deciduous species).

Whereas endodormancy is like a ‘do-not-disturb’ setting, ecodormancy is more analogous to an alarm clock that tracks warm temperatures rather than time. This alarm clock is set off once buds have experienced a cumulative amount of warm weather. Metabolic profiling has been used to quantify changes in metabolite concentrations as buds progress through each dormancy phase (e.g., Chmielewski and Götz 2022). From this, researchers have found that genes associated with synthesis of GAs and auxins (*GA20ox*, *GA3ox*, and members of the *YUCCA* gene family) may gradually become more active during ecodormancy (Canton et al. 2021). These hormones promote the initiation of cell division and elongation. After the release of ecodormancy, there are no internal biological controls restricting growth, and bud break is reliant only on environmental conditions.

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11.3.3 Drivers

The primary drivers of spring budburst and leaf-out after the chilling requirement has been fulfilled are warm temperatures (forcing) and photoperiod (Liang 2019), as these factors together promote ecodormancy release. Temperature varies throughout the day, but daily maximum (T_{MAX}), minimum (T_{MIN}), and average (T_{AVG}; calculated from hourly measurements) temperatures are highly correlated, so it is a matter of some debate just "which" temperature is most important as a driver of forcing. For example, Meng et al. (2020) found that using diurnal T_{MIN} and T_{MAX} rather than T_{AVG} better explained observations of satellite-derived start-of-spring dates. This may be due to (1) the potential ability of trees to accumulate chilling and forcing temperatures at the same time from diurnal T_{MIN} and T_{MAX} respectively, and (2) the fact that global land-surface T_{MIN} has been increasing 1.4 times faster than T_{MAX} in the last 50 years (Stocker 2014; Meng et al. 2020), and T_{AVG} tends not to capture this diurnal temperature fluctuation, nor the uneven pace of warming between T_{MIN} and T_{MAX}.

To track forcing, often a combination of these temperature measurements is used to calculate heat units known as growing degree days (GDD). The purpose of GDD is to sum the heat energy a plant receives over a given period and relate this forcing quantity to the progression towards a phenophase. The basic formula for growing degree days from daily data is $GDD = \max\left(\left[\frac{T_{MAX} + T_{MIN}}{2}\right] - T_{BASE}, 0\right)$ where T_{BASE} is the minimum temperature for forcing to be effective. Growing degree hours can be similarly calculated from hourly data. T_{BASE} is both species- and phenophase-specific (McMaster and Wilhelm 1997), but values between 0 and 5°C are typical. A common approach to inferring the influence of drivers on specific phenophases is to examine how interannual variations in spring phenophases correlate with interannual variations in forcing over a particular window, or to use model-based approaches (Basler et al. 2016; Hufkens et al. 2018). Such approaches of analyzing interannual variation are useful for understanding long-term changes in spring phenology.

11.3.4 Long-term Trends

In recent decades, warmer and advancing spring temperatures, and thus faster GDD accumulation, have generally led to earlier spring leaf-out, although sometimes with devastating impact as early leaf-out has occasionally been followed by widespread frost damage (e.g., Gu et al. 2008). The five longest deciduous tree phenological records from around the world show that on average, spring phenophases (budburst, leaf-out, and flowering) occurred six to 30 days (mean ± standard error; 14.14 ± 9.09 days) earlier over the period from 1985 to 2020, whereas negligible trends were observed over previous decades-to-centuries (Vitasse et al. 2022). These unprecedented phenological shifts have been referred to as "the great acceleration." Numerous other studies published over the last 25 years have presented supporting results (Badeck et al. 2004; Cohen et al. 2018; Melaas et al. 2018; Fig. 11.4), although exceptions to these general trends may be seen at sites where springtime warming is negligible, even as mean annual temperature is increasing (Fig. 11.5). Figure 11.4 shows that trends in spring phenology can differ by ecoregion due to the unevenness and complexity of spring warming patterns in some regions (Melaas et al. 2018). Furthermore, there is speculation over whether spring phenology will continue to track warming temperatures at a uniform rate, as there are several interacting environmental and biological factors that control dormancy release (Zhou et al. 2023), and uncertainties remain about whether chilling or photoperiod controls might place an upper limit on how far budburst can advance (Lange et al. 2016; Gauzere et al. 2017).

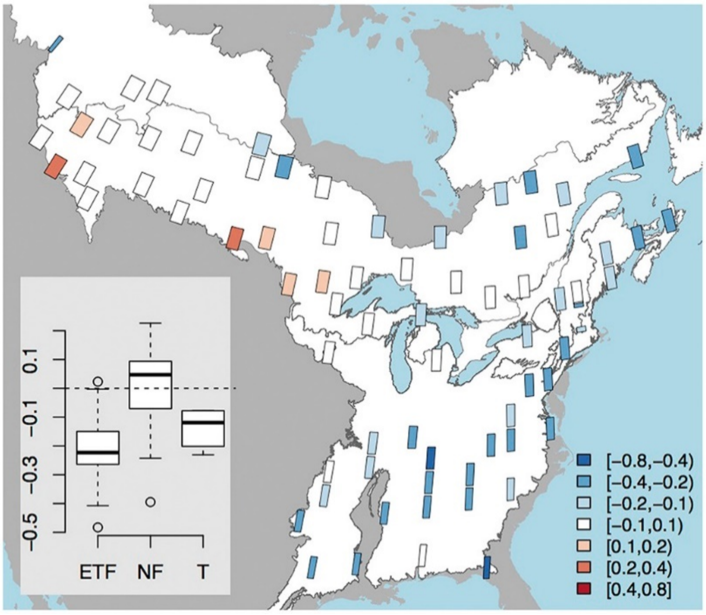

Fig. áá.é Average trend in spring onset date from fixedǫeffects regression models calibrated using Landsat land surface phenology data. Boxplots show the distribution of spring onset dates for each ecoregion: ETF ǿ Eastern Temperate Forests, NF ǿ Northern Forests, and T ǿ Taiga. The date for start of season is earlier on average across ETF's. Source: Melaas et al. ąóáį.

As described above, some studies have shown an inverse relationship between the chilling and forcing accumulation needed to break endo- and ecodormancy, respectively. That is, deeper and extended chilling typically results in a reduction in the forcing sum and duration needed to achieve budburst (Cooke et al. 2012; Laube et al. 2014; Hänninen 2016). However, warming winters may be slowing the progression of chilling accumulation, delaying the transition from endodormancy to ecodormancy (Laube et al. 2014; Fu, Piao et al. 2015; Fu, Zhao et al. 2015; Asse et al. 2018). More forcing may then be required to counterbalance suboptimal or inadequate chilling, potentially delaying ecodormancy release and budburst (Fu, Piao et al. 2015; Beil et al. 2021; Zhang et al., 2022).

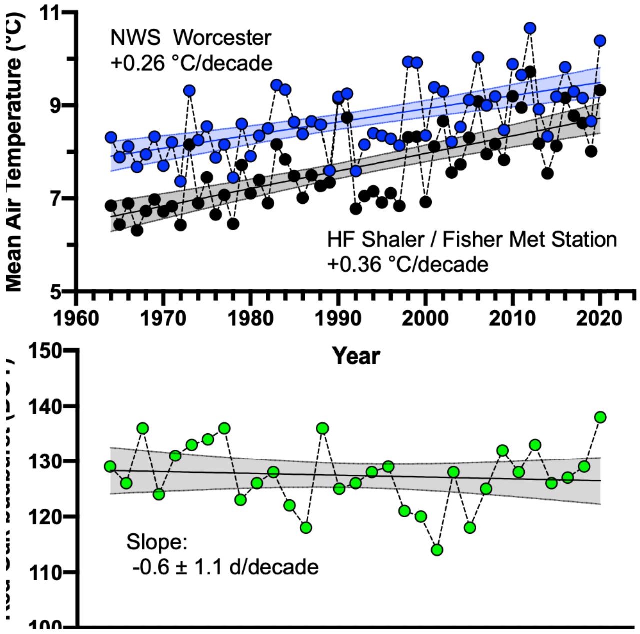

Fig áá.ę Although ĮtopÓ mean annual temperature in central Massachusetts ĮNational Weather Station data from Worcester, and Harvard Forest data Shaler/Fisher Meteorological StationÓ is rising at ≈ó.ą°C per decade over the last ęó y, ĮbottomÓ red oak budburst dates have not advanced significantly since áįįó. One explanation for this is that although there is a strong relationship between AprilǫMay temperature and red oak budburst date Įǫą.í ± ó.ę days per degree of warmingÓ, there has been a nonǫ significant warming trend in April and May over the áįįǫąóąó period. Data from the Harvard Forest Data Archive ĮHFǫóóá, HFǫóóąÓ.

Some studies have reported changes in budburst temperature sensitivity (although Keenan et al. (2020) have argued this is a flawed metric; see section *11.5.2*), which has been attributed to several factors, including changes in the *start* of endodormancy. For example, observed warming-driven delays in autumn leaf senescence (see sections *11.4.3* & *11.4.4*), and the associated induction of endodormancy may be shifting the overall dormancy period later. In other words, warming effects on spring budburst may be partially offset by the previous autumn occurring later, potentially leading to a shift towards *both* later dormancy onset *and* release (Beil et al. 2021; see Fig. 11.6). In summary, temperature can have varying effects on spring phenology depending on when warming occurs, but driver interactions can modify the amount of chilling and forcing that trees receive.

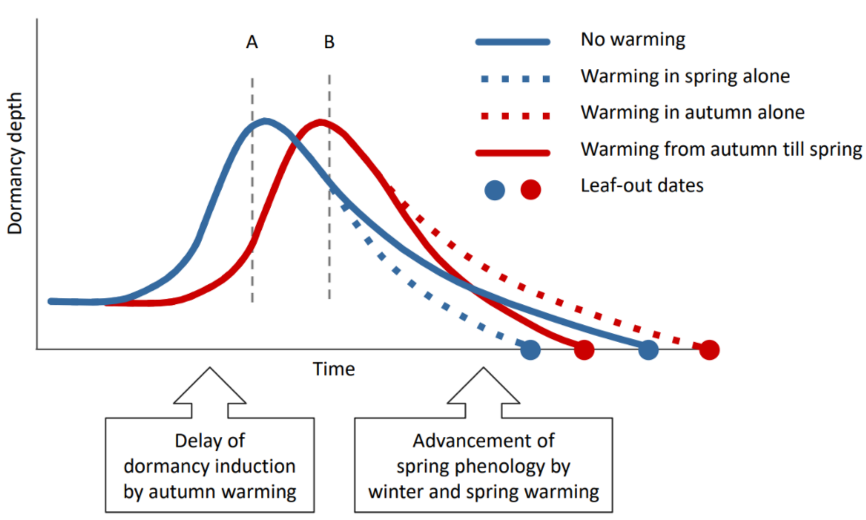

Fig. áá.ę Schematic illustrating the effect of temperature at different times of the year on bud dormancy induction and release. Autumn warming typically causes a delay in reaching maximum dormancy depth. Delayed endodormancy release therefore somewhat offsets advances due to autumn and spring warming. In years when autumn temperatures are not above average and endodormancy is not delayed, springọonly warming may result in the earliest possible spring phenology scenario. If delayed endodormancy release due to autumn warming is not followed by spring warming, this may actually delay the onset of leaf out. Source: Beil et al. ąóąá.

11.3.5 Driver Interactions

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In mesic temperate deciduous forests, precipitation frequency can have an indirect effect on spring phenology by modifying plant exposure to chilling and forcing temperatures. Wu et al. (2022) found that decreasing precipitation frequency may reduce the time it takes to achieve chilling and forcing requirements. Reduced precipitation frequency was found to be associated with concurrent reductions in cloud cover. With reduced cloud cover, the amount of radiation absorbed during the day and emitted at night by the Earth’s surface were both found to increase, leading to warmer days and cooler nights. This indirect temperature effect of precipitation frequency could continue to advance spring phenology, in addition to precipitation frequency (paired in some cases with increases in precipitation intensity), which is becoming a consistent meteorological pattern across northern regions with climate change (Trenberth 2011).

Temperature effects on budburst and other phenophases can also be influenced by photoperiod, and for that reason some studies have modified the general equation for GDD so that a given GDD sum has more of an effect on phenological transitions when days are long than when days are short. In six European temperate species, Fu et al. (2019) found that forcing requirement for leaf-out has an inverse relationship with photoperiod length in addition to and independent of the effects of chilling. It has been hypothesized that this may serve as a mechanism to optimize plant growth, as it adds extra protection from late spring frost while also ensuring that after budburst, trees are exposed to the maximum amount of solar radiation. This way, if forests experience a warm winter and break endodormancy later in the season (during a time of longer photoperiod), their forcing requirement will be reduced (Fu et al. 2019). In cases where these mechanisms fail or warmer conditions lead to early, but inopportune, leaf-out, frost exposure can have multiple ecological consequences.

11.3.6 Ecological Consequences of Frost Exposure

Immediately following budbreak, the new leaves of deciduous trees are particularly sensitive to stress. Potential stress factors include not just high temperatures (heatwave) and drought, but also cold temperatures and, potentially, frost damage. At a minimum, cool spring temperatures can slow the development of, or even damage, bud and leaf tissues, ultimately delaying leaf maturity (Gunderson et al. 2012). When new leaves are exposed to below-freezing temperatures, leaf necrosis resulting from frost damage can significantly reduce future photosynthetic uptake and forest productivity; there is also an immediate carbon and nutrient cost of dead tissues. Trees at higher elevation may be especially at risk of frost damage due to the occurrence of lower minimum temperatures compared to lower elevations, but phenological timing is critical. For example, Hufkens et al. (2012) found that mid-elevation trees were hit hardest by spring frost, as foliage on lower-elevation and early-budburst trees was more mature and hence less susceptible to damage, and higher-elevation and late-budburst trees had not yet leafed out.

In years of mid-spring frost, plants that require less chilling or forcing and leaf-out earlier (pre-frost) may be at a competitive disadvantage to plants that flush later in the season (post-frost). However, in years with exceptionally warm growing seasons and no spring frosts, late-flushing plants may be the ones at a competitive disadvantage, as early-flushing plants would have a greater duration of photosynthetic activity and enhanced C economy (Hufkens et al. 2012; Fu et al. 2019; Zettlemoyer et al. 2019; Chu et al. 2021). Early- and late-flushing plants can fall within the broader categories of species or endemism, i.e., this increased competition could occur interspecifically or between native and non-native plants (Hufkens et al. 2012; Gallinat et al. 2015; Zettlemoyer et al. 2019). There is some suggestion that because of increased spring temperature variability, exposure of expanding leaves to frost has become more frequent in recent decades and this trend may persist through the coming decades (Gunderson et al. 2012; Liu et al. 2018; Ma et al. 2019).

11.3.7 Future Directions

Through observational, experimental, and modeling studies, researchers have come a long way in understanding the drivers of spring phenology, but many questions on the subject remain. The metabolic pathways and biological mechanisms responsible for dormancy release have yet to be definitively elucidated, and particularly how these mechanisms may vary among species is largely unknown. More experimental studies are needed to quantify the thresholds of hormone concentration or gene expression associated with dormancy release, as well as how hormones interact to promote growth (Yu et al. 2020). In addition, more studies – particularly phenological experiments that push organisms to the edge of, or beyond, the past ranges of environmental variability – are needed to test various theories that attempt to explain why spring phenology may become less sensitive to warming in the future. However, one important way in which our understanding of mesic temperate deciduous forest phenology has advanced over the last decade is recognition of the importance of autumn, the "neglected season," in the context of both tree physiology and forest ecology (Gallinat et al. 2015). Only through understanding what drives changes at both the start *and* the end of the growing season can we obtain a complete picture of how overall growing season length and thus net primary productivity will change under future climate conditions.

11.4 Autumn Phenology

Throughout summer, chlorophyll and chloroplasts are abundant in leaf tissue. Chlorophyll production gradually slows down to a stop as autumn approaches, and all chlorophyll is eventually broken down (Mattila et al. 2018). Other pigments such as carotenoids, xanthophylls, and anthocyanins begin to dominate in concentration once senescence begins. During the growing season, the orange, yellow, and red appearances of these respective compounds are masked by the higher concentration of green-colored chlorophyll. Once chlorophyll degradation increases during senescence, the fiery pigments we associate with fall start to take prominence. Whereas budburst, leaf-out, and leaf expansion occur in rapid and easily-identifiable succession in spring, the process of autumn senescence, from onset to leaf coloration and ultimately leaf drop, is more drawn-out and variable not only among species but also among individuals of the same species (Lee et al. 2003; Panchen et al. 2015). It is also cryptic, in that many of the associated processes (e.g., abscission) are not visible to the human eye. At the same time that changes in the canopy are occurring, the cell walls of new stemwood xylem tissues start to thicken and are lignified in early autumn, and generally wood growth cessation is concurrent with when leaves begin to senesce, but this can change depending on drought and site characteristics (Dox et al. 2020). Several temperate deciduous fruit trees, such as *Malus* spp. (apple) and *Pyrus* spp. (pear), produce fruit in the fall prior to senescence, and these fruits are important food resources for animals, insects, and humans.

11.4.1 Nutrient Resorption

Prior to leaf abscission, nutrients in leaves are reabsorbed and stored in woody tissues. Nutrient resorption can be optimized, to some degree, by adjusting the timing of autumn leaf senescence. Optimization is important because nutrients stored in woody tissues are needed for new leaf formation and early wood growth in the following spring (Keskitalo et al. 2005), but there are obvious carbon costs to premature resorption. Nutrients that are not successfully resorbed in fall would need to be replenished from the soil and allocated to new tissues. This would affect the carbon uptake capacity of trees in early spring, and potentially beyond (Estiarte and Peñuelas 2015). When autumn is delayed or the progression of leaf senescence is slowed due to warm autumn temperatures, the efficiency of nutrient resorption can be slightly enhanced (Estiarte and Peñuelas 2015). However, warm autumns accompanied by drought or sudden frosts could become more frequent, resulting in abscission of green leaves before proper senescence and nutrient reabsorption occur (Gunderson 2012; Estiarte and Peñuelas 2015; Liu et al. 2018).

In the context of resorption from senescing leaves, the most important plant nutrients consist of nitrogen (N), phosphorous (P), potassium (K), and sulfur (S). Calcium and magnesium are also vital nutrients, but are often accreted, or transported into rather than out of, senescing leaves (Killingbeck 2004). Most N comes from degradation of chloroplasts, with lesser amounts contributed by nucleic acids, amino acids, chlorophyll, and cytosolic proteins. P is found mostly in the form of soluble inorganic orthophosphate ions, but can also be derived from organic macromolecules such as RNA, DNA, and lipids (Wieczorek et al. 2022). Senescent leaves that achieve "complete" resorption retain <0.05% (0.5 mg g^{-1}) N and <0.04% (0.4 mg g^{-1}) P (Estiarte et al. 2022).

K is present as soluble ions (K^{+}), so it is easily transported and does not require breakdown of macromolecules to be resorbed. S can be isolated from the primary S-containing amino acids, methionine and cysteine (Estiarte and Peñuelas 2015). In the case of nutrients derived from macromolecules, several hydrolytic enzymes carry out the degradation process to isolate these nutrients. As chlorophyll degrades during senescence, mitochondria fueled by glucose in leaves provide the energy needed for hydrolytic and nutrient translocation processes (Estiarte and Peñuelas 2015).

11.4.2 Dormancy Induction

In response to shortening photoperiod, the concentration of ABA in leaves begins to increase. ABA promotes growth cessation via synthesis of hydrolytic enzymes, which break carbon-carbon bonds of the polysaccharides that make up cell walls in the abscission zone of the leaf petiole (Kozlowski and Pallardy 1997). Full leaf abscission occurs once enough of these polysaccharides are broken down.

ABA accumulation also gradually causes blockages within plasmodesmata, or pores between adjacent plant cells that allow for cell-to-cell communication. These blockages cut off symplastic intercellular communication of growth hormones between cells. To assess the photoperiodic control of dormancy onset, maintenance, and release, Tylewicz et al. (2018) conducted an experimental knockout of the gene that controls ABA signaling in aspen trees. In their experiment, both control and gene-knockout aspens ceased growth and set bud after 4 weeks of 8-hour (short) photoperiod without chilling. Exposure to short photoperiod continued for an additional 7 weeks. After subsequent exposure to 16-hour (long) photoperiod without chilling, aspens with the gene knockout, which had reduced sensitivity to ABA and reduced plasmodesmata blockages, then experienced bud-break in 11 to 15 days. Control aspen, however, maintained dormancy. ABA signaling is therefore essential for maintaining proper dormancy regulation and preventing premature budbreak in response to lengthening photoperiod (Tylewicz et al. 2018). So, photoperiod exhibits dominant but variable control over dormancy onset (depending on species-specific critical daylength), and pre-season and autumn climate can modify this timing. These drivers interact to shape community-level patterns of autumn leaf phenology.

11.4.3 Drivers

Cooling temperatures, decreasing photoperiod, and water limitation are the main drivers of (earlier) autumn senescence (Gill et al. 2015). The relative importance of these drivers may vary by location, and geographic factors such as latitude are associated with large-scale gradients in the timing of senescence. As discussed, photoperiod exhibits dominant control, but the start and progression of senescence are modified by temperature (Tylewicz et al. 2018). In the absence of water stress, cooler autumn temperatures tend to hasten senescence, whereas warmer autumns tend to delay senescence (Delpierre et al. 2009; Fu et al. 2018). Water stress tends to drive earlier senescence, but this may be less pronounced in mesic climates (Fu et al. 2018).

Additionally, the effects of water stress may depend on day vs. night temperatures and could also differ among species. Chen et al. (2020) and Wu et al. (2018) found that day and nighttime temperatures have contrasting, indirect effects on water stress in autumn. Warmer autumn *daytime* temperatures could exacerbate water stress, as higher temperatures promote greater transpiration of water vapor during photosynthesis. This would theoretically promote earlier senescence, but it could also increase atmospheric water vapor and result in higher nighttime temperatures, potentially *delaying* senescence by slowing chilling accumulation. Warmer autumn *nights* could then extend the time needed to achieve chilling requirements for senescence, which might drive later senescence. But whether this is a widespread phenomenon has not been established. The papers by Chen et al. (2020) and Wu et al. (2018) also found that the effects of water stress on senescence are variable from species to species. Isohydric species, e.g., black walnut (*Juglans nigra*), that have a very conservative water regulation strategy may senesce earlier in response to warming autumn days and enhanced drought. Anisohydric species, e.g., white oak (*Quercus alba*), which have less strict water regulation and are more drought resistant, may experience delayed senescence in response to warming nighttime temperatures (Wu et al. 2022). Even in mesic regions, autumn drought conditions could become more prevalent not only from warming autumns and changes in precipitation patterns, but also if rapid spring development and vegetation activity draws down water resources, leading to dry conditions later in the growing season (Wu et al. 2018; Wolf et al. 2016). In fact, there are several factors related to spring phenology that can influence the timing of autumn, as we discuss in the next section.

11.4.4 SOS-EOS Correlation and Lagged Effects of Spring

Many studies have found that there is a significant positive correlation between interannual variation in start-of-season (SOS) and end-of-season (EOS) timing in mesic temperate deciduous tree species, despite the weak decadal trend of slightly delayed autumn phenology (Zhu et al. 2012; Fu et al. 2014; Keenan and Richardson 2015; Peng et al. 2021; Marqués et al. 2023). There are several potential explanations for this phenomenon. For one, it has been hypothesized that the positive relationship is attributable to a genetically predetermined constraint on leaf lifespan (Lim et al. 2007; Hänninen and Tanino 2011; Kikuzawa and Lechowicz 2011; Fu et al. 2019; Marqués et al. 2023). If leaf lifespan has a fixed duration, then an earlier start to a leaf's life can be expected to result in an earlier senescence as well, subject to modification by other environmental factors.

In contrast, the sink limitation hypothesis states that once trees have accumulated a saturating amount of carbon, the inability to use additional carbon may trigger the cessation of photosynthesis and the onset of leaf senescence (Zani et al. 2020). There is abundant evidence that tree growth is more limited by environmental factors acting on the processes controlling growth than by the environmental supply of carbon to support growth (Körner 2003). As atmospheric CO_2 increases, temperatures rise, and leaves emerge earlier – stimulating photosynthesis – trees may reach this critical C capacity sooner and senesce earlier (Zani et al. 2020; Marqués et al. 2023; Zohner et al. 2023).

The sensitivity of autumn senescence to different drivers, specifically temperature, may vary throughout the growing season (Archetti et al. 2013). Recently, Zohner et al. (2023) found that increases in photosynthetic activity and temperatures occurring *before* the summer solstice (times of lengthening photoperiod) tend to induce *earlier* senescence, while increases in temperature *after* the solstice (shortening photoperiod) tend *not* to influence the start of EOS. Incorporating pre-solstice vegetation activity as a driver, Zohner et al. (2023) therefore postulated that earlier, more productive springs may result in earlier autumn start date, while warming autumn temperatures may slow the progression of leaf senescence, resulting in a later autumn end date. This supports sink and/or nutrient limitation theories more so than the leaf longevity theory (Zohner et al. 2023). This study is consistent with Jiang et al. (2022) who found the duration of autumn leaf senescence is sensitive to autumn temperatures, whereas the onset of senescence is not sensitive to temperature.

In summary, temperature, water availability, photoperiod, and lagged effects of spring may have contrasting effects on autumn phenology, depending on when they occur on monthly to daily timescales and when certain species are most sensitive to them (Yan et al. 2021). What we do know for certain is that, on average, warmer autumns tend to delay senescence progression and drought tends to advance senescence, but responses are divergent across species and regions (Zhang et al. 2015; Wang et al. 2022).

11.4.5 Long-term Trends

There has been a weak but statistically significant global trend of delayed autumn senescence across mesic temperate deciduous forests in recent decades (Sparks and Menzel 2002; Ibáñez et al. 2010; Beil et al. 2021; Calinger and Curtis 2023). Trends in autumn phenology have been highly variable in both direction and magnitude across geographic regions and species. However, a recent experimental study showed a larger temperature response in autumn leaf senescence compared to spring leaf out in European beech saplings (Fu et al. 2018). In addition, there is support from several studies (Taylor et al. 2008; Richardson et al. 2010; Gunderson 2012; Zhu et al. 2012; Marchin et al. 2015; Calinger and Curtis, 2023) that photosynthetic activity will continue to extend further into fall in response to warming temperatures in the future, so long as water does not become limiting. If temperate deciduous trees hold their leaves longer, and continue to photosynthesize later into autumn, this could result in increased ecosystem productivity and possibly enhanced long-term carbon sequestration. This scenario has been hypothesized (e.g., Richardson et al. 2010) based on patterns of interannual variation in the duration of photosynthetic uptake and total annual gross photosynthesis estimated from tower-based CO_2 flux measurements. Decadal-scale trends would also seem to support this hypothesis, although it is unclear whether such increases can be sustained under future climate scenarios; this is a topic of debate and much current research (Rollinson 2020; Zani et al. 2020).

11.4.6 Uncertainty and Future Directions

There are fewer autumn phenological studies compared to spring; as of late 2014, autumn studies only account for 27.9% of climate change leaf phenology publications in the Scopus database, whereas spring studies make up the remaining 72.1% (Gallinat et al. 2015). In Web of Science, searching for “spring phenology” within the last five years of literature yields a result of 749 papers, whereas searching “autumn phenology” only yields 192 papers. This is likely due to the complexity of autumn drivers and the more gradual progression of autumn phenophases compared to spring phenophases (Gallinat et al. 2015). Varying quantifications of autumn phenometrics (e.g., leaf coloration or drop percentage, canopy greenness inflection point, chlorophyll content) from study to study make it difficult to establish a unified study design (Gordo and Sanz, 2009; Gallinat et al. 2015). A metanalysis of 56 autumn phenology studies identified 24 different methods of estimating EOS date (Gill et al. 2015). Autumn phenology studies with similar, generalized results and predictions are difficult to come by due to this lack of standardized EOS date determination, and also due to autumn driver complexity.

There are ongoing debates about which drivers are the most influential on EOS, whether future autumns will be delayed or advanced, and how this will affect forest carbon budgets (Piao et al. 2008; Zhang et al. 2020; Lu and Keenan 2022). It is also unclear how nutrient availability and nutrient gathering strategies contribute to EOS timing. Some argue nutrient limitation should induce earlier senescence, but conflicting studies have shown no effect of nutrient availability on senescence (Sigurdsson 2001; Weih 2009; Fu et al. 2019; Dox et al. 2020; Vitasse et al. 2021). In the future, unified study designs, phenophase definitions, and protocols are needed to fill the current knowledge gaps on autumn phenology. In addition, we need to develop a wider array of process-oriented models for autumn phenology, we need climate manipulation experiments that place more of an emphasis on understanding autumn phenology, and – important for improving both autumn *and* spring studies – we need improved methods of scaling up phenological observations from species to landscapes (Piao et al. 2019).

11.5 Modeling and Prediction

Phenology models can be classified as either empirical or process-based. Empirical models are informed strictly by observations of phenology and their drivers, and the statistical relationship between them (e.g., degree-day models). Process-based models, however, incorporate mechanisms of plant biology that precede phenological changes (see Section 11.5.2). Process-based models are typically more realistic because biological mechanisms can have varying responses to drivers, and empirical models take into account past climate and phenological data to inform future predictions (Piao et al. 2019). There is much room for improvement in modeling spring and autumn phenology. The following sections highlight the issues with current modeling approaches, as well as potential solutions.

11.5.1 Methodological and Empirical Flaws

There are several methodological flaws that may harm the accuracy or realism of phenological predictions. For example, Keenan et al. (2020) pointed out that the widely used “temperature sensitivity” metric (i.e., change in phenophase date per degree of warming) is highly sensitive to the date range over which “temperature” is calculated. The apparent temperature sensitivity is higher when temperature is integrated over a longer period, and smaller when the integration period is shorter. This is because mean temperatures taken over longer integration periods (e.g., monthly, seasonal, or annual) are less variable from year to year compared to mean temperatures integrated over shorter periods (e.g., daily or weekly). Thus, it is difficult to compare temperature sensitivities across studies, and this also implies that the estimated temperature sensitivity in response to interannual variability would be different from the estimated temperature sensitivity in response to long-term warming.

In support of this idea that *when* certain temperatures occur matters, Friedl et al. (2014) showed that trees across the northeastern U.S. are sensitive to the nature and timing of net thermal forcing. 2012 was warmer overall than 2010, but trees exhibited earlier leaf out in 2010 due to net forcing occurring earlier in the season compared to 2012. If we were to integrate temperature over the entire spring in each of these years, we would be omitting the importance of the timing of net thermal forcing on spring leaf out. While current spring models are fairly accurate, incorporating the above modeling insights could improve spring predictions under current climate conditions. However, to account for how physiological processes will respond to novel conditions under climate change, the current modeling paradigm may need to shift toward process-based models informed by data from both observational and experimental studies (Hänninen et al. 2019; Asse et al. 2020).

Current inverse modeling approaches favor selection of less-complex models that work well under current conditions, but they may not be accurate for future conditions when processes like chilling become more limiting under climate change (Chuine et al. 1999; Linkosalo et al. 2008; Vitasse et al. 2011; Asse et al. 2020). However, to produce such dynamic, process-based models, we need to collect much more observational and experimental data on physiological, metabolic, and microscopic scales to see how these processes will react to weather extremes (Hänninen et al. 2019). In addition, we need datasets that would allow us to falsify current models and justify adding complexity to new models.

Another problem with current modeling approaches is that linear models are sometimes applied to biological processes that have a natural nonlinear response to a climatic variable. For example, the apparent reduction in temperature sensitivity of spring phenology is accounted for if leaf-out predictions are generated using log-transformed inputs (Wolkovich et al. 2021). This implies that warming temperatures are not changing the underlying biological processes associated with chilling and forcing accumulation, but that spring-leaf out naturally responds to higher temperature in a nonlinear, logarithmic fashion. More testing of null and alternative models is needed to avoid improper assumptions of statistical anomalies as changes in biology (Wolkovich et al. 2021).

11.5.2 1- vs. 2-Phase Models and the Problem of Endodormancy

As winters warm, budburst predictions may suffer if we cannot accurately model physiological endodormancy break. Modeling this and other physiological processes is important because trees may break endodormancy later than expected, or not at all, if chilling duration and intensity continue to decrease (Chuine et al. 2016). Interestingly, current models parameterized with ecodormancy break alone (one-phase models) predict budburst with the same or better accuracy than models that also incorporate endodormancy break and/or dormancy onset (two-phase models) (Vitasse et al. 2011; Basler 2016; Chuine et al. 2016). This means that most species are currently receiving enough chilling in the winter for endodormancy break. However, models that are calibrated and parameterized with endodormancy dates may predict budburst more accurately than models that do not in regions where warming autumn and winter temperatures may cause endodormancy failure (insufficient chilling) in the future (Chuine et al. 2016). For that reason, using two-phase models is especially relevant for species at the warmer edge of their distribution, e.g., Northern Hemisphere populations at the southern edge or lower-elevation limit of their species distributions (Vitasse et al. 2011; Chuine et al. 2016; Sánchez-Salguero et al. 2017).

The issue with this is that very few data are available on endodormancy break. Endodormancy break must be estimated on a species-to-species basis through a time-consuming and destructive experimental process, in which twigs are sampled and monitored individually under *ex-situ* forcing conditions (Chuine et al. 2010; 2016). Some recent studies have explored changes in the transcriptomic profiles of fruit trees during endodormancy and ecodormancy to gain a better understanding of how the timing of release and concentration of certain hormones are responsible for endodormancy release (Yang et al. 2021; Sapkota et al. 2023), but until more endodormancy data become available for more species, it will be difficult to generate accurate two-phase spring models applicable to many species.

11.6 Impacts on Ecosystem Processes

11.6.1 Biosphere-Atmosphere Interactions

The timing, size, and location of energy, water, and carbon fluxes in deciduous broadleaf forests are closely intertwined with phenology (Fig. 11.7; Pielke et al. 1998; McPherson 2007; Richardson et al. 2013; Moon 2020). These fluxes have implications for ecosystem productivity, weather and atmospheric circulation patterns, planetary boundary layer (PBL) dynamics (Fig. 11.8), climate change feedback loops, and thus phenology itself (Schwartz 1992; Richardson et al. 2013; Li et al. 2023).

For example, latent heat fluxes (energy consumption via evapotranspiration (ET)) increase alongside spring photosynthetic activity until they peak in summer. The decreased ratio of sensible heat (convective heat transfer) to latent heat flux after leaf-out has a cooling effect and slows the rate of temperature increase in spring (Fig. 11.8; Schwartz 1992; Piao et al. 2019; Li et al. 2023). Leaf expansion also has an indirect effect on temperature via increased cloud production from enhanced ET. These processes work in tandem to change the height of the PBL (Fig. 11.8).

The emergence of leaves can also drive changes in global weather patterns. In the Northern Hemisphere, the latitudinal component of wind shifts from northerly to southerly just prior to bud-break date, and continues blowing more southerly post-budburst, affecting meteorological circulation patterns (Schwartz 1992). Due to this switch to southerly wind patterns, the favorable transport of accumulated water vapor (a greenhouse gas) from mesic temperate forests to northern latitudes has led to rapid warming of the Arctic zones (Francis and Skific 2015; Xu et al. 2020).

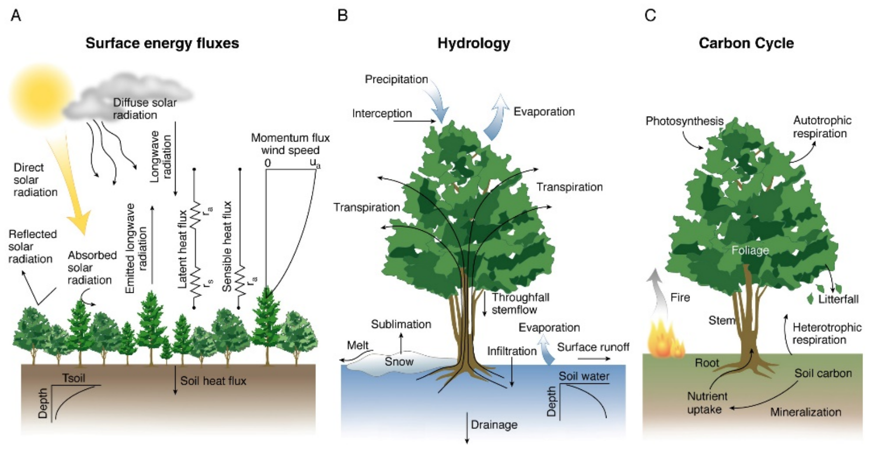

Fig. áá.í Schematics of ĮAÓ surface energy fluxes, ĮBÓ the hydrologic cycle, and ĮCÓ the carbon cycle in temperate deciduous forests. These core biogeophysical and ǫ chemical cycles change alongside canopy phenology, as leaf out, leaf drop, and photosynthetic activity drive changes in surface albedo, evapotranspiration, carbon and nutrient flux, and turbulent mixing of the atmosphere. Source: Bonan ąóóį.

11.6.2 Carbon Cycling

Growing season length is a strong predictor of forest net ecosystem productivity (NEP) (Churkina et al. 2005; Richardson et al. 2010). Several studies have shown that increased photosynthesis significantly outpaces increases in respiration resulting from an overall extended growing season (Richardson et al. 2010; Keenan et al. 2014; Teets et al. 2023). In addition, several land surface phenology studies have shown evidence of delayed autumn contributing more days to the lengthening growing season than earlier spring (Zhu et al. 2012; Zhao et al. 2013; Garonna et al. 2014), but earlier spring tends to contribute more to annual forest gross primary production (GPP) than delayed autumn due to increases in autumn respiration that partially offset increases in autumn photosynthesis (Wu 2013; Keenan 2014; Teets et al. 2023). From the analysis in Richardson et al. (2010), we have also learned that the relationship between growing season length and forest carbon uptake may be more sensitive across sites than across time. This means that looking at changes in growing season length across sites rather than looking at interannual variability of growing season length at individual sites may tell us more about potential for long-term changes in forest NEP (Richardson et al. 2010).

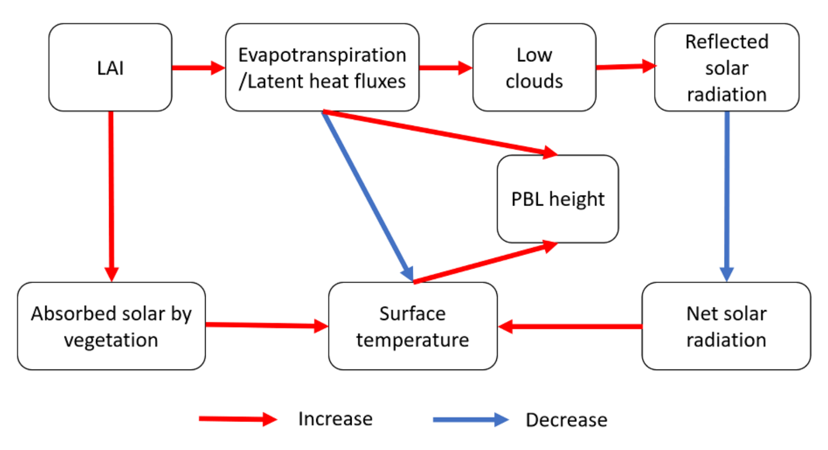

Fig. áá.į Conceptual diagram showing the relationships between PBL states and increases in canopy physiological activity in temperate deciduous forests. Spring leaf expansion tends to raise PBL height, but the degree and timing of increase or decrease are dependent on location, temperature profiles, and leaf phenology. Source: Li et al. ąóąá.

However, how the "growing season" is defined can matter for how we understand and model carbon uptake via plant productivity. For example, growing season can be defined by leaf phenology, phenology of xylogenesis, periods of positive NEP, or periods in which climate is permissible for growth (Körner et al. 2023). Most commonly in the current literature, growing season is defined by leaf phenology, but this should not be directly associated with forest NEP because xylogenesis phenology can often lag behind leaf phenology, and also because in some years, NEP can be negative overall (Körner et al. 2023; Arend et al. 2024).

11.7 Conclusions

In the last decade, researchers have uncovered much about the mechanisms and effects of deciduous forest phenology, from the phytohormone scale to the global climate scale. In this chapter, we have discussed how hormones are regulated to initiate and sustain different spring and autumn phenophases, how drivers interact to shape phenological timing, current phenology modeling paradigms, and how phenology affects the climate system, biogeochemical cycles, and ecosystem ecology. We have discussed key knowledge gaps, and identified ways in which these gaps might be addressed in future studies. Filling these gaps is crucial for the prediction of temperate deciduous forest phenological changes in the Anthropocene.

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