BULLETIN

Shifting Phenology in a Changing Climate

MARCH 30, 2017 / BY JENNIFER HUSHAW

Phenology is the study of the seasonal rhythms of plants and animals, especially the timing of natural cycles as related to weather and climate. It is a sensitive indicator of climate change, with far reaching implications for ecosystem processes, productivity, and even the global carbon budget.

In previous bulletins, we discussed how phenology is expected to shift due to a warming climate, leading to a whole host of direct and downstream impacts. In this bulletin, we delve into more detail and reveal how phenology of boreal and temperate trees, in particular, has already shifted and is likely to continue changing, as well as the potential ramifications for forestry. We also discuss some of the major questions that still remain to be answered, such as which species are most well-suited to track warming trends and maintain optimal phenology in the future.

Background

WHY PHENOLOGY MATTERS

Phenology is sometimes described as "the pulse of the planet" because of the way it mediates seasonal and annual processes related to carbon, water, and nutrient cycling. By controlling the timing and extent of leaf area, flowering, leaf fall and other developments, phenology directly influences productivity, growth, evapotranspiration, runoff, decomposition, and mineralization (Richardson et al 2013). It is also relevant on a global scale because it influences vegetation-related feedbacks to the climate system, such as:

- **Albedo**, e.g. changes in reflected solar radiation when deciduous forests move from leaf-off to leaf-on conditions
- **Canopy conductance**, e.g. changes in the amount of leaf area that affect transpiration rates and CO_2 uptake
- **Flows of water and energy**, e.g. increased transfer of water vapor to the lower atmosphere following leaf-out
- **CO_2 fluxes**, e.g. changes in the balance between forest canopy photosynthesis and ecosystem respiration

Through these feedbacks, phenology not only influences regional weather patterns, but can also affect long-term global climate (Richardson et al 2013). All this means that **phenology has massive implications for global change science, ecosystem processes, and land management (including forestry).**

For a more detailed description of climate feedbacks, including those associated with forests, revisit the June 2015 bulletin, Uncertainty in Climate Change and Forest Response: Part I.

SEASONAL SIGNALS

Temperate and boreal trees go into dormancy every winter to protect their tissues against damage from cold temperatures, creating an annual cycle where dormancy is induced in the fall and released in the spring. These phenological shifts are cued and mediated by four primary factors:

- Degree of warming in spring
- Onset of cold temperatures in fall
- Degree and duration of winter chilling
- Photoperiod (i.e. day length relative to night length)

(Way & Montgomery 2015)

The diagram in Figure 1 illustrates how this process generally unfolds. In autumn, shorter days and lower temperatures induce endodormancy (an internally, genetically controlled, set state of inactivity), where growth ceases. Trees can only resume growth in the spring after they receive a signal that winter has ended, in the form of exposure to cool, non-freezing temperatures (also known as 'chilling'). Although the amount of chilling required varies from species to species, it is a necessary prerequisite to move the tree into ecodormancy (a state of inactivity imposed by unfavorable environmental conditions), which is when they become sensitive to temperature and photoperiod cues. Once a certain amount of warming (i.e. degree-days) have been accumulated or certain photoperiod thresholds are met, the plant is released from ecodormancy and experiences the onset of bud burst, leaf unfolding, flowering, etc. (Basler & Körner 2014).

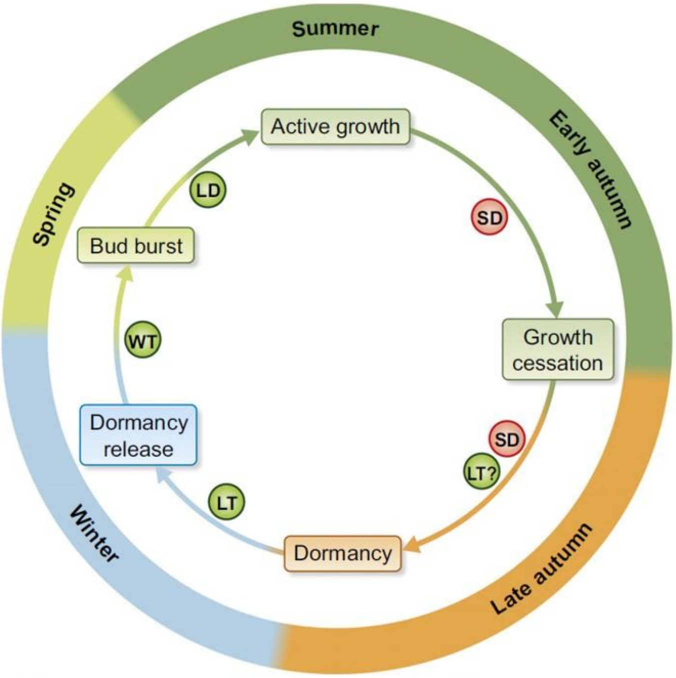

Figure 1: Annual growth cycle in trees, where WT = warm temps, LT = low temps, SD = short days, and LD = long days.
Source: Singh et al 2017

Clearly, much of this process is strongly mediated by temperature, including the rate at which buds and leaves develop after dormancy, but photoperiod and chilling are critical controls as well. As we discuss in a later section, the degree to which particular species are sensitive to chilling and/or photoperiod has the potential to constrain how well they track warming temperatures and adapt to changes in climate.

VARIABLE SENSITIVITY TO SEASONAL CUES

Complexity arises because the relative importance of the four factors listed above varies by species, genetic makeup, gene expression (i.e. phenotype), successional strategy, and region of origin (Way & Montgomery 2015; Basler & Körner 2014; Körner & Basler 2010; Kramer et al 2017; Laube et al 2014; Rohde et al 2011). It also depends whether we are considering spring or fall phenology, since the latter is generally more sensitive to photoperiod than the former (Way & Montgomery 2015).

For example, one key factor is sensitivity to photoperiod. Trees that rely strongly on day length to signal phenology, rather than temperature cues, have certain advantages and disadvantages. Relying on photoperiod can help trees guard against leafing out too early and experiencing late season frosts, but responding to temperature gives trees the flexibility to take advantage of the extended period for photosynthesis (and the associated growth increase) offered by earlier onset of the frost-free season. As a result, species that are sensitive to photoperiod are less likely to experience earlier leaf out in response to warming. A common example is *Fagus sylvatica* (European beech), which is known to be particularly sensitive to photoperiod (less so to temperature) and has demonstrated a low level of variability in the timing of leaf unfolding from year to year, despite variability in temperature (Basler & Körner 2014). See Table 1 (below) for the categorization of some common species from across the globe.

Table 1: Species grouped according to whether bud burst is sensitive or insensitive to photoperiod based on literature review (equivocal indicated studies showed inconsistent results), from Way & Montgomery 2015, Table 1.

Photoperiod Sensitive	Photoperiod Insensitive		Equivocal
Abies alba (European silver fir)	*Abies homolepis* (Nikko fir)	*Robinia pseudoacacia* (black locust)	*Acer pseudoplatanus* (sycamore maple)
Alnus glutinosa (European alder)	*Acer negundo* (box elder, ash-leaf maple)	*Rubus idaeus* (American red raspberry)	*Aesculus hippocastanum* (horse chestnut)
Alnus incana (gray alder)	*Acer saccharum* (sugar maple)	*Sorbus aucuparia* (rowan/Europ.mountain ash)	*Betula pendula* (European white birch)
Betula pubescens (downy birch)	*Acer tataricum* (Tatarian maple)	*Sorbus intermedia* (Swedish whitebeam)	*Corylus avellana* (European hazel)
Cornus alba (tatarian dogwood)	*Amorpha fruticose* (false indigo bush)	*Symphoricarpos albus* (common snowberry)	*Picea abies* (Norway spruce)
Fagus sylvatica (European beech)	*Carpinus betulus* (European hornbeam)	*Ulmus glabra* (wych elm/Scots elm)	*Pseudotsuga menziesii* (Douglas fir)
Fraxinus Americana (white ash)	*Cornus mas* (cornelian cherry)	*Ulmus macrocarpa* (large-fruited elm)	*Quercus robur* (English oak)
Juglans regia (English walnut)	*Fraxinus chinensis* (Chinese ash)	*Ulmus minor* (field elm)	
Liquidamber styraciflua (American sweetgum)	*Fraxinus excelsior* (European ash)	*Ulmus parvifolia* (Chinese elm/lacebark elm)	
Pinus strobus (Eastern white pine)	*Fraxinus pennsylvanica* (green ash)	*Ulmus pumila* (Siberian elm)	
Pinus wallichiana (Himalayan pine)	*Juglans ailantifolia* (Japanese walnut)		
Populus tremula (European poplar)	*Larix decidua* (European larch)		
Prunus padus (European bird cherry)	*Pinus nigra* (Austrian pine)		
Quercus alba (white oak)	*Pinus sylvestris* (Scots pine)		
Quercus bicolor (swamp white oak)	*Populus tremuloides* (quaking aspen)		
Quercus petraea (sessile oak)	*Prunus avium* (sweet cherry/wild cherry)		
Salix x smithiana (Smith's willow)	*Prunus serotina* (black cherry)		
Tilia cordata (small-leaved lime)	*Quercus rubra* (northern red oak)		

Phenology: An Indicator of Change

People have been recording the timing of the seasons through plant phenology for centuries. The longest known records date back to the 9th century and describe the flowering of Japanese cherry trees, which are now blooming earlier than at any point in the last 1200 years (Primack et al 2009). Over the past few decades, phenology has increasingly been recognized as a useful indicator of long-term ecosystem change (Richardson et al 2013) and is now a prominent part of efforts to track the impact of a warming climate. In fact, the U.S. Global Change Research Program (USGCRP) includes the start of spring as one of their 14 initial indicators of climate change.

SPRING

Spring phenology is well-understood and has been more extensively studied than autumn, in large part because it is easier to measure and detect the changes associated with phenomena like leaf out and flowering than the gradual process of fall senescence.

Evidence from ground-based and satellite studies (mostly in the Northern Hemisphere) shows spring advancement for “hundreds of plant and animal species in many regions” and, globally, spring has been advancing earlier at an average rate of around 3.3 (± 0.87) days per decade for tree species, with larger changes generally at higher latitudes (Settele et al 2014). Indeed, a recent analysis of 25 years of satellite data detected an advance of 14.5 days in the start of the growing season in northern high latitude areas (> 45ºN) (Jeganathan et al 2014). Advance in the timing of spring onset in temperate trees over the last four decades can be attributed to warming temperatures (Richardson et al 2013).

In the U.S., there has been a general trend toward earlier springs since 1984 (USGCRP). In fact, the year 2012, which was the hottest year on record for the U.S., stands out as the earliest spring start (Figure 2). Although, that record may soon be broken because “2017 is shaping up to be two to three weeks earlier than 2012 in many parts of the country” (NPN 2017) and up to three weeks earlier than normal (compared to 1981-2010) in some locations in the southeast (Figure 3).

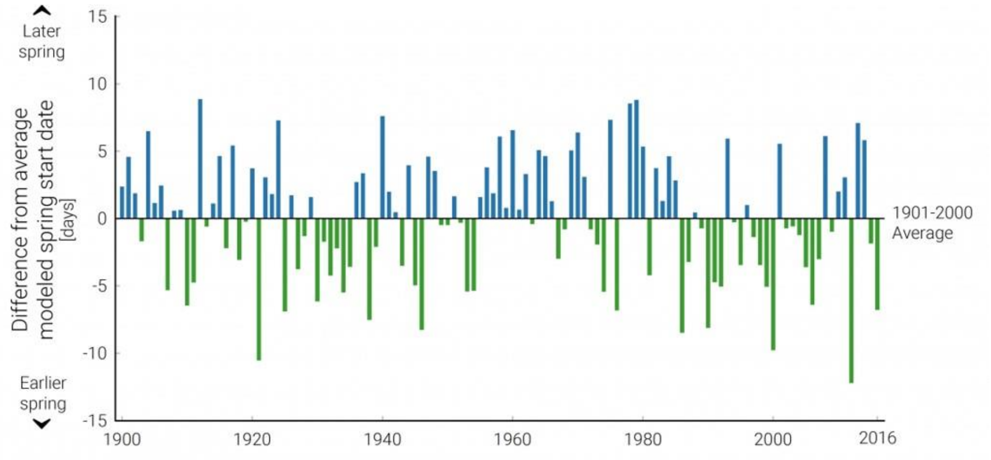

Figure 2: Annual start of spring for the contiguous United States.
Source: USGCRP (www.globalchange.gov/browse/indicators/indicator-start-spring)

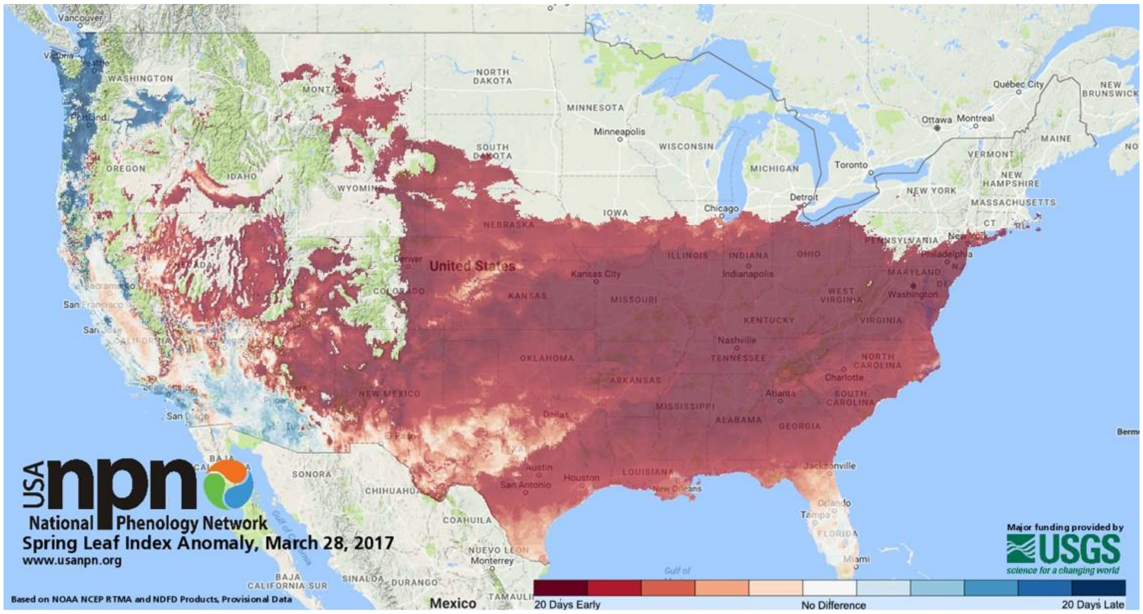

Figure 3: Spring Leaf Index Anomaly for March 2017, where warmer colors indicate earlier onset of spring and cooler colors indicate later.
Source: NPN (www.usanpn.org/data/spring)

AUTUMN

The effect is less pronounced than for spring, but there have been documented delays in autumn senescence in European and North American temperate forests of 3-4 days per decade since 1982 (Rosenzweig et al 2007; Richardson et al 2013). The work by Jeganathan et al (2014), mentioned above, also detected a 16-day delay in the end of the growing season in high northern latitudes over the last several decades.

GROWING SEASON

Figure 4: Length of growing season in the contiguous 48 states, 1895-2015.
Source: EPA's "Climate Change Indicators in the United States" (Data source: Kunkel, K.E. 2016 update to data originally published in Kunkel et al 2004.)

These shifts in phenology, combined with a lengthening of the frost-free season, have increased the length of the growing season in many places (as we discussed in [a previous bulletin]). In the U.S., it has increased by as much as ten days since the 1980's (EPA; Figure 4), with some parts of the country experiencing increases of up to 50 days in the period since 1895 (EPA; Figure 5). This has the potential to be a boon for the productivity of many ecosystems, including forests, e.g. research suggests lengthening the growing season by 5-10 days may increase annual net primary productivity of forest systems, by as much as 30% (Jackson et al 2001) and other studies have shown that a difference of just one week in the timing of canopy development can mean a 20% difference in photosynthetic production from year to year (Myneni et al 1997).

Shifting Phenology in a Warmer World

Given the importance of temperature for signaling tree species phenology, what are the implications of climate change for our forests? This is an important question because changes in phenology have implications for productivity, survival, inter-species competition, pest and disease impacts, wildlife, and more. A review of the latest science suggests the following:

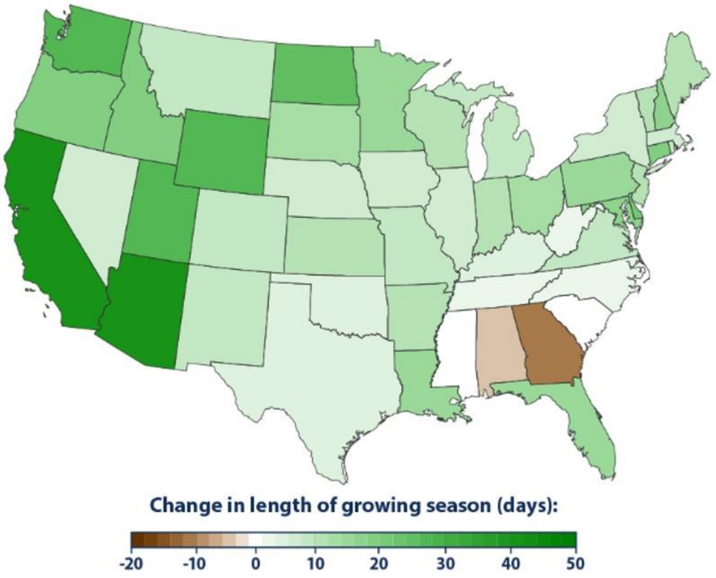

Figure 5: Change in length of growing season by state, 1895-2015.
Source: EPA's "Climate Change Indicators in the United States" (Data source: Kunkel, K.E. 2016 expanded analysis of data originally published in Kunkel et al 2004.)

Opportunities

- Overall extension of the growing season will increase forest productivity
- Pioneer species (which have lower chilling requirements) may benefit from warmer winters
- Many species demonstrate phenotypic plasticity, or an ability to shift their phenology to take advantage of warmer temperatures
- Most species are likely to experience decreases in frost damage over time (on average)

Challenges

- Many species are likely to experience increased frost damage in some part of their distribution, particularly on the margins (even if they see a decrease on average)
- Invasive species tend to have lower chilling requirements and less sensitivity to photoperiod, so they will benefit from warmer winters and take advantage of earlier spring warmth
- Species composition may change due to phenologically-induced changes in understory light conditions that influence seedling survival
- Certain characteristics, such as sensitivity to photoperiod, appear to be genetically determined, so some species will be limited in their ability to response to warming temperatures (especially in autumn when phenology is more strongly controlled by photoperiod)

It depends…

- For some species, milder winters will make it difficult to meet chilling requirements—leading to delays in spring phenology that may reduce their competitive advantage and growth potential, but also reduce their risk of late season frost
- There will be changes in competitive advantage between species, based on varying ability to track warmer temperatures and take advantage of a longer growing season

(Laube et al 2014; Kramer et al 2017; Morin & Chuine 2014; Körner & Basler 2010; Basler & Körner 2014; Fu et al 2015; Chen et al 2017)

Emerging Research & Remaining Questions

The relationship between a warming world and forest phenology may seem straightforward—warmer temperatures, longer growing season, increased growth and productivity. However, a review of the current science reveals that it's not quite that simple. Tree species, and even particular provenances, have unique sensitivities to the various seasonal cues, which makes it challenging to anticipate exactly how the timing of phenological events will shift on a local scale. Since there are many factors at play in determining how a particular species or site will change, it will be important to watch your own forest carefully to see which species are responding most effectively to warming temperatures.

As new research emerges, we will be better able to accurately pin down likely changes and identify the potential impacts for forest health, productivity, and composition. The following lists major uncertainties in the science, on-going research needs, and key questions that remain to be answered:

- Relative importance of photoperiod versus temperature
- Species-specific responses
- Degree of phenotypic plasticity of particular species
- Change in likelihood of frost damage (overall)
- Better understanding/more research into climate change impacts on autumn phenology
- Tension between scientific evidence for constraints on phenology (e.g. photoperiod sensitivity) and demonstrated species plasticity
- Potential role of air humidity as a control on phenology
- Improved phenological models that are more generalizable
- Improved representation of phenological processes in terrestrial ecosystem models
- Extremes can fundamentally alter phenological response—posing a challenge for prediction
- Effective temperature range for chilling is only vaguely known for forest trees
- Potential role of soil water in mediating phenology
- Lack of an underlying ecological or physiological scheme that differentiates between photoperiodically sensitive and insensitive trees species—to facilitate prediction under future climate

(Basler & Körner 2014; Way & Montgomery 2015; Tansey et al 2017; Kramer et al 2017; Morin & Chuine 2014; Richardson et al 2013; Laube et al 2014b; Delpierre et al 2016; Carter et al 2017; Delpierre et al 2017)

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