



Interspecific and interannual variation in the duration of spring phenophases in a northern mixed forest



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ARTICLE INFO

Keywords:

Deciduous trees
Coniferous trees
Bud-open
Leaf-out
Full leaf unfolded
Spring phenophase duration
Local temperature

ABSTRACT

A wide range of intra- and interspecific variation occurs in spring leaf phenology as a result of biotic factors such as, life strategy, ecological niche and genetic adaptation, and abiotic factors such as environmental condition. Whereas knowing when the start of bud-burst occurs is necessary for determining the beginning of the growing season, and the subsequent start of carbon uptake, the duration of phenophases is equally important (to estimate the rate of carbon uptake, for example), but rarely reported. Here, we investigate variation in the timing and duration of 3 key phenophase categories (bud-open, leaf-out, full-leaf unfolded) from a range of 8 broadleaf and 2 conifer species in a mixed forest in northern Wisconsin, USA over a 5-year period. As expected, the start of each phenophase category varied across species and years and an earlier start to one phenophase did not necessarily result in an earlier start to subsequent phenophases nor did it mean a faster or slower progression. Ecological niche was not always a useful predictor of the timing or duration of the spring phenology season. The spring phenology season from bud-burst to full leaf open for the entire forest community took an average of 13 days ranging from 12 to 18 days across species. Bud-open and leaf-out lasted an average of 4 days whereas, full-leaf unfolding lasted 5 and again there were variations among species. Full leaf unfolded for *A. incana* lasted significantly ($p < 0.001$) longer than other species. Variation in the duration of the spring phenology season among years closely tracked local seasonal air-temperature based on growing degree hours (GDH). These results could be used to help determine the relationship between phenology and the potential for carbon storage in early spring in a mixed forest and highlight the value of direct field observation data at species level, the detail of which cannot, at present, be captured by satellite remote sensing.

1. Introduction

The spring season in temperate forests is marked by the phenological development of leaves, from dormant buds, to leaf emergence through to full leaf expansion and canopy development. This annual progression is primarily driven by an increase in temperature in spring although a lengthening of the photoperiod and other environmental parameters (such as precipitation and soil moisture availability) may also influence the rate of leaf development (Downs and Borthwick 1956; Myking and Heide 1995; Stevens et al., 1995; Murray et al., 1989; Bertin, 2008; Caffarra et al., 2011; Pletsers et al., 2015; Shen et al., 2015; Liu et al., 2016). Therefore, when environmental conditions are

suitable bud-burst, leaf-out and leaf expansion will occur but because these conditions vary from one year to the next so too does the timing and duration of the phenology season. Furthermore, not all forest species respond to the same environmental stimulus e.g., rising spring temperature, at the same rate (Lechowicz, 1984; Donnelly et al., 2006; Lopez et al., 2008; Caffarra and Donnelly 2011; Vitasse et al., 2009; Yu et al., 2015) and given the wide range of tree species that make-up a forest community the greening process tends to vary over space and time. Both biotic and abiotic factors combine to influence the overall timing of green-up, making predictions of the timing and the rate of phenological progression a challenging task.

Nevertheless, it is important to be able to determine both the timing

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and rate of leaf development due to its functional significance in overall ecosystem dynamics. Leaf phenology is pivotal to a range of forest processes as, for example, it determines the start, end and length of the growing season which in turn determines the annual amount (and rate) of CO₂ removal from the atmosphere by photosynthesis and subsequent storage in biomass (White et al., 1999; Piao et al., 2007; Richardson et al., 2013; Keenan et al., 2014; Hufkens et al., 2016). Furthermore, leaves are an important element in many food-webs and changes in timing and progression may impact resource availability for herbivores and higher trophic level organisms (Harrington et al., 1999; Visser and Holleman, 2000; Visser et al., 2004; Both et al., 2009; Donnelly et al., 2011, 2014). The timing of the start and end of the phenology season has been successfully determined at a range of scales from the individual tree by direct *in situ* observation (Peñuelas and Filella, 2001; Menzel et al., 2006; Donnelly et al., 2006; Fu et al., 2015; Zheng et al., 2016) to landscape and continental scales by remote sensing using either satellites (Myneni et al., 1997; Justice et al., 1985; Moulin et al., 1997; Zhang et al., 2001; Liang et al., 2011; Li et al., 2015) or digital cameras (Huete et al., 2002; Richardson et al., 2011; Sonnentag et al., 2012; Zhang et al., 2014) capable of recording the greening process. In recent years, much attention has been given to capturing the timing of bud-burst and leaf fall to establish if changes have occurred over time due to climate change and for determining the start and end of the carbon uptake period. Equally important, but much less reported, is knowing the rate at which these events progress. Establishing the timing and duration of subtle transitions from one phenophase to another may not, at present, be captured by remotely sensed means due to the coarseness of both spatial and temporal resolution, cloud contamination and sensor technology limitations. Whereas temporal resolution and cloud cover may be addressed using the geostationary ABI with 5-min observations the spatial resolution is still too coarse to accurately detect subtle transitions in phenophases. Therefore, continuous *in situ* monitoring is necessary to observe how changes in environmental condition, such as rising temperature, impact the timing and rate of progression of leaf phenology which, in turn, may have wider reaching consequences for overall forest dynamics. However, since continuous *in situ* monitoring cannot be accomplished universally, a balance must be reached between spatially extensive *in situ* surveys and remote sensing approaches.

Given the large variation in the timing and duration of leaf-out among different species, populations of the same species, individuals of the same species and even on different locations on the same plant it is challenging to estimate the overall characteristics of spring phenology in a forest community. Therefore, we wanted to test the hypothesis that particular ecological characteristics (opportunistic vs late successional, determinate vs indeterminate growth, ring porous vs diffuse porous wood) of individual species would be reflected in the timing and duration of key phenophases that, in turn, could be used to predict the overall duration of the spring phenology season in a mixed northern forest community. Furthermore, since phenological progression is driven by rising seasonal temperature we tested a range of temperature parameters (average temperature and Growing Degree Hours) as potential drivers of the timing and duration of individual species' spring phenology. In order to test these hypotheses we examined the timing and duration of 3 key phenophase categories (bud-open, leaf-out, full-leaf unfolded) from a range of 8 broadleaf and 2 conifer species in a mixed forest in northern Wisconsin over a 5-year period from 2006 to 2010. Subsequently, we correlated the results with temperature parameters derived from a nearby flux-tower.

2. Materials and methods

2.1. Study site

The study area has been extensively described in Schwartz et al. (2013). In brief, the study site is located in a mixed deciduous (70%)

Table 1

Scientific and common names of the tree species used in this study together with the number (range across years) of individuals with sufficient data, ecological niche (US Forest Service) and wood anatomy type. Not all species present at both sites some only found in the North Study Area (NSA) and some in the South Study Area (SSA). Growth habit D – determinate (single growth flush in spring) and I indeterminate (several spurts during growing season).

Species	Number	Wood anatomy type	Adaptation	Growth habit
<i>Broadleaf, late successional</i>				
<i>Acer saccharum</i> Sugar Maple	81–121 NSA 7–12 SSA	Diffuse porous	Shade tolerant	D
<i>Acer rubrum</i> Red Maple	38–79 NSA 19–82 SSA	Diffuse porous	Moderately shade tolerant	D
<i>Tilia Americana</i> American Basswood	9–22 NSA	Diffuse porous	Moderately shade tolerant	D
<i>Broadleaf, early successional</i>				
<i>Populus tremuloides</i> Quaking Aspen	10–17 NSA 29–114 SSA	Diffuse porous	Shade intolerant	I
<i>Populus grandidentata</i> Big-toothed Aspen	5–7 NSA	Diffuse porous	Shade intolerant	I
<i>Alnus incana</i> Speckled Alder	5–29 SSA	Diffuse porous	Moderately shade intolerant	I
<i>Betula papyrifera</i> White Birch	8–24 SSA 5 NSA	Diffuse porous	Shade intolerant	I
<i>Betula alleghaniensis</i> Yellow Birch	6 NSA 6–7 SSA	Diffuse porous	Shade intolerant	I
<i>Needle</i>				
<i>Abies balsamea</i> Balsam Fir: Late successional	24–51 SSA 7 NSA	Non-porous	Shade tolerant	D
<i>Larix laricina</i> Tamarack: Early successional	11 NSA	Non-porous	Shade intolerant	D

and coniferous (30%) forest community near Park Falls (45.9347° N, 90.4486° W) in northern Wisconsin, USA. There were two (the North and the South) 625 m x 625 m study areas each containing 144 plots and 3 individual trees at each resulting in 864 trees. In addition, 24 *Tilia americana* (American Basswood) trees were included in the observation campaign bringing the total number of trees being monitored to 888. Details of the individual species number, wood anatomy type, adaptation and growth habit are presented in Table 1.

2.2. Phenological data

Spring phenology monitoring was carried out from 2006 to 2010 (see Schwartz et al., 2013 for a detailed description). For the purposes of the current study we used data from three phenophase categories; bud-burst (300–390), leaf-out (400–490) and full leaf unfolded (500–590) (Table 2). Each category was subdivided into 4 percentage classes (< 10%, 10–50%, 50–90% and > 90%) representing progressively more advanced stages of development. Each category and appropriate subdivision were combined to give a phenophase value on a particular day. For example, a tree assigned a phenophase value of 350 meant that between 50 and 90% of the buds were open whereas, a value of 500 indicated that < 10% of the leaves on the tree were fully unfolded. The reason for omitting phenological stages prior to bud-burst e.g., dormant buds and buds swollen, was due to the high number of missing values in these categories as a result of the difficulty of observing these stages accurately in the upper canopy. Furthermore, we only used individual trees for which a complete set of observations i.e., all phenophase categories from 300 to 590, was available in any particular year and we only used species which had a minimum of five individuals with a complete record at a particular site. This resulted in the number of individuals and species varying from year to year. We

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