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Predicting autumn phenology: How deciduous tree species respond to weather stressors

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ABSTRACT

Shifts in the timing of autumnal leaf coloration and leaf drop in temperate forests with climate change can have substantial impacts on community and ecosystem processes (e.g. altered carbon/nitrogen cycling and biotic interactions). However, the environmental control of autumn phenology remains significantly understudied in striking contrast to spring phenology. In this study, we used linear mixed effects model with ground-based phenology observations in northeastern USA and found that both weather stressors (e.g. heat- and drought-stress and heavy rainfall) during the growing season and spring phenology significantly affected inter-annual variation in autumn phenology of twelve dominant deciduous tree species. While warm temperatures and drought lead to later fall phenology for most species, heavy rainfall and heat stress lead to earlier leaf coloration and leaf drop. We also found that the phenological sensitivities to weather stressors are diversely species-specific. Under future climate change projections, we predicted that greater summer heat-stress in the future will cause abbreviated leaf coloration seasons for most species. Our mixed-effects modeling framework suggested that accounting for phenological variations among individual trees, species and sites largely improved model predictions, which should not be overlooked in phenological model development. Our study improves our understanding of how species-specific autumnal phenology responds to weather stresses, and describes a new modeling framework to investigate both inter-annual phenological changes and local variations among trees, species, and sites. Our predictions on autumn phenological shifts will help in assessing the effects of climate change on forest community and ecosystem processes in the future.

1. Introduction

Climate change to date has caused dramatic plant phenological shifts in both spring and autumn in temperate regions around the world (Doi and Takahashi, 2008; Körner and Basler, 2010; Polgar and Primack, 2011; Jeong et al., 2011; Visser, 2016), which can in turn influence ecological processes substantially, including C and N cycling, hydrology, demography, and biotic interactions (Vitasse et al., 2009; Fridley, 2012; Pépino et al., 2013; Estiarte and Peñuelas, 2015; Thackeray et al., 2016; Elmore et al., 2016). For example, delays in autumn phenology (i.e. timing of leaf coloration and leaf drop) that lead to extended growing seasons, may increase the risk of freezing damage from early autumnal frosts, preventing reabsorption of nutrients from leaves and altering nutrient cycles (Niinemets, 2010; Norby et al., 2003; Richardson et al., 2013). Changes in the phenology of foliage coloring may alter cues for animal behaviors such as avian migration (Ellwood et al., 2015). The timing of fall foliage color change also impacts the multi-billion dollar fall foliage ecotourism industry, especially in the northeastern United States (Rustad et al., 2012; Spencer and Holecek, 2007). However, the autumn phenological responses in plants to environmental changes remain poorly understood (Gallinat et al., 2015). The important key environmental factors that affect plant autumn phenology and the species-specific responses thereto, other than frost or chill-stress, remain largely unknown.

Our knowledge of the environmental control of leaf senescence in temperate deciduous woody plants has changed surprisingly little over the past 60 years (Lim et al., 2007; Samish, 1954). In the 2007 review by Lim and colleagues (Lim et al., 2007), the factors that most likely affect the timing of leaf coloration and drop in the autumn were suggested to include day length, heat, cold, drought, wetness, nutrient and pathogen attack. But previous studies of environmental influences on autumn phenology have focused only on the effects of autumn chilling, frost, and/or day length (Archetti et al., 2013; Delpierre et al., 2009; Gill et al., 2015; Jeong and Medvigy, 2014); one exception is the study

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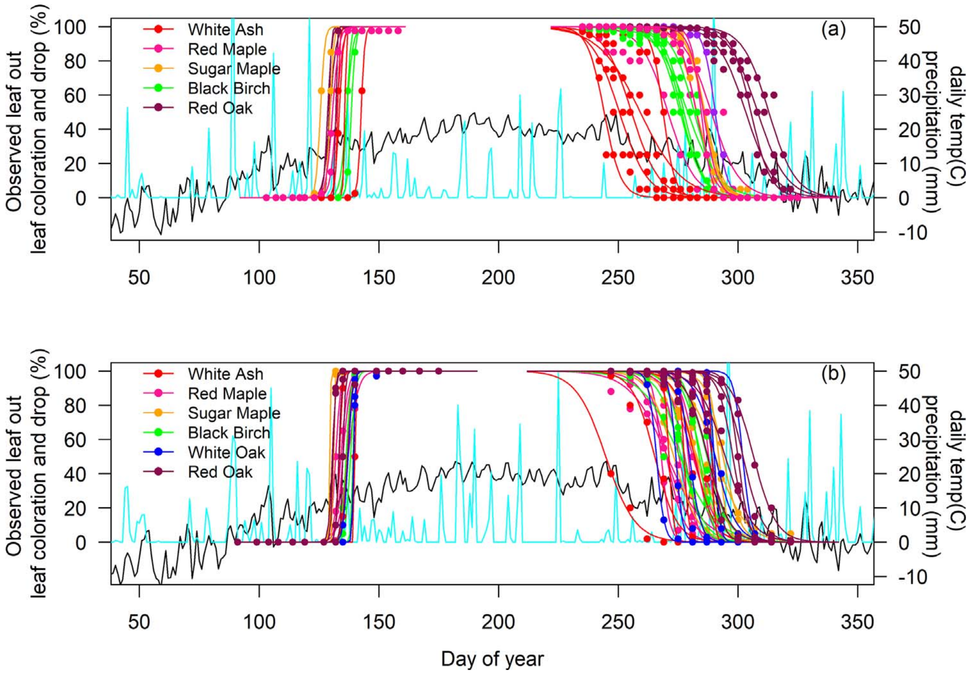

Fig. 1. Observed leaf phenology of 6 common deciduous tree species in spring and autumn in 2014 at the RMP site in UCONN Forest (a) and at Harvard Forest (b). Each color indicates one species. Each dot is one observation. Each curve line is a logistic curve fitted to the observations. Daily temperatures (°C) and precipitation (mm) are shown as black and light blue lines respectively. Spring phenology shows leaf unfolding, and autumn phenology includes leaf coloration and leaf drop. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

considering the effects from precipitation (Estrella and Menzel, 2006), and our own study of fall phenology based on satellite-derived data (Xie et al., 2015b). Although physiological experiments have reported the effects of a subset of these factors (i.e. temperature, day length, and drought) on plant leaf coloration and leaf drop (Fracheboud et al., 2009; Naschitz et al., 2014; Rosenthal and Camm, 1997), few studies have identified the relative importance of contributing factors or quantified their effects (Estrella and Menzel, 2006). Our previous study found that other than decreasing temperature in autumn, moisture conditions and extreme weather events across the entire growing season (e.g. drought, heat stress and heavy rainfall) all have significant effects on the timing of autumn senescence at the forested landscape scale (Xie et al., 2015b). However, it is unclear how autumn phenology of temperate forest tree species responded individually to these environmental stresses. Since forest tree species with various physiological structures and mechanisms showed different strategies in response to environmental changes (Diez et al., 2012; Tang et al., 2016), we expect diverse sensitivities to stressors in autumn phenology among forest tree species. While temperate forest communities may change species compositions spatially, understanding species-specific autumn phenology responses to potential environmental stressors is critical to assessing phenological shifts and impacts for the forest communities at regional and landscape scales (Richardson et al., 2013; Jeong and Medvigy, 2014).

Diverse phenological responses among plant species were widely recognized by previous studies (Estrella and Menzel, 2006; Primack et al., 2009; Vitasse et al., 2009). However, variations in phenology among individuals or locations within tree species are often overlooked in phenological modeling, even though they have been noted (Crawley and Akhteruzzaman, 1988; Ne'Eman, 1993; Delpierre et al., 2017). The risk of ignoring phenological variation among individuals and locations that may be associated with ontogeny or sites effects, could result in overestimates or underestimates of phenological variation driven by diverse environmental factors, which in turn will lead to biased predictions of phenological responses to environmental changes. Thus, instead of treating phenology of each individual or at each location as independent of each other, we expect the new modeling framework developed here not only to explain species-specific autumn phenological responses to the important climate/weather factors, but also to include the variation in phenology due to site and individual effects.

In addition, positive relationships between spring and autumn phenology were reported (Fu et al., 2014; Keenan and Richardson, 2015), which indicates a more complex mechanism of phenological responses of plants and points to our general lack of understanding of the phenological activities of plants across the entire growing season. Since both spring and autumn phenologies of plants are likely responding to climate change, the influences of phenological changes in the spring should also be included in building models to explain phenological changes in autumn in response to climate change.

Our study focuses on autumn phenology from the beginning of leaf coloration through the end of leaf drop for 12 dominant deciduous tree species of northeastern United States forest communities. The objectives are: 1) to identify important climatic and weather factors affecting autumn phenology of deciduous tree species; 2) to quantify species-specific phenological responses to the important environmental factors; 3) to develop a modeling framework to explain phenological variation inter-annually and among trees, species and sites; and 4) to predict future autumn phenological shifts of deciduous tree species driven by projected climate change.

2. Methods

2.1. Phenology and climate data

We used two sets of phenology ground observations in this study. One is from five sites in Connecticut USA (2012-2014), and the other is from Harvard Forest (1993–2014) (Fig. 1 and Table S2). To collect phenology data in Connecticut, we established 5 plots (25m × 50 m) that stratified local site conditions (i.e. variation in soil and soil moisture and species composition) in the natural forest landscapes in and around the University of Connecticut (UCONN) campus. We randomly selected 88 individuals of eight dominant tree species differentially present in five sites (Table S2). The eight species were: red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), black birch (*Betula lenta*), pignut hickory (*Carya glabra*), shagbark hickory (*Carya ovata*), white ash (*Fraxinus americana*), white oak (*Quercus alba*), and red oak (*Quercus rubra*). In total 88 individual adult trees were observed from 2012 to 2014. We observed leaf phenology for each individual, including bud burst, leaf unfolding, leaf coloration and leaf drop (cf. Figs. 1 and S1). Observations were conducted twice a week (Table S1)