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The timing of autumn senescence is affected by the timing of spring phenology: implications for predictive models

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Abstract

Autumn senescence regulates multiple aspects of ecosystem function, along with associated feedbacks to the climate system. Despite its importance, current understanding of the drivers of senescence is limited, leading to a large spread in predictions of how the timing of senescence, and thus the length of the growing season, will change under future climate conditions. The most commonly held paradigm is that temperature and photoperiod are the primary controls, which suggests a future extension of the autumnal growing season as global temperatures rise. Here, using two decades of ground- and satellite-based observations of temperate deciduous forest phenology, we show that the timing of autumn senescence is correlated with the timing of spring budburst across the entire eastern United States. On a year-to-year basis, an earlier/later spring was associated with an earlier/later autumn senescence, both for individual species and at a regional scale. We use the observed relationship to develop a novel model of autumn phenology. In contrast to current phenology models, this model predicts that the potential response of autumn phenology to future climate change is strongly limited by the impact of climate change on spring phenology. Current models of autumn phenology therefore may overpredict future increases in the length of the growing season, with subsequent impacts for modeling future CO_2 uptake and evapotranspiration.

Introduction

Many aspects of ecosystem function are sensitive to variability in the timing of phenological events, leading to multiple feedbacks to the climate system (Richardson *et al*., 2013). Ecosystem

carbon, water, and nutrient cycling are all strongly dependent on phenology (Gu *et al*., 2003; Noormets, 2009), as are competitive and mutualistic interactions (Cleland *et al*., 2007), species distributions (Chuine, 2010), and trophic dynamics (Bartlam-brooks *et al*., 2013). Phenology is sensitive to changes in climate, and thus has been highlighted as one of the primary indicators of climate change (Stocker & Dahe, 2013). The sensitivity of phenology to future climate change therefore has important implications for climate, ecosystems, and the services they provide (Schröter *et al*., 2005).

Despite the importance of phenology, current terrestrial ecosystem models perform poorly at predicting phenological events (Keenan *et al*., 2012; Richardson *et al*., 2012). Environmental drivers control spring phenology in a predictable manner (Jeong *et al*., 2012; Migliavacca *et al*., 2012), although no single modeling approach has to date proven unequivocally superior and prediction across broad spatial domains or under novel climate regimes remains challenging (Richardson *et al*., 2013). Autumn phenology, however, has received much less attention. This is in large part due to the attenuated nature of autumn senescence, which leads to difficulties for deriving autumn senescence dates from remote sensing (Garrity *et al*., 2011; Klosterman *et al*., 2014), and for the identification of coherent environmental controls on autumn senescence (Archetti *et al*., 2013).

Temperature, photoperiod, and precipitation are considered to be the primary controls of autumn phenology of deciduous forest trees (Körner & Basler, 2010; Rohde *et al*., 2011; Archetti *et al*., 2013). Warmer temperatures are expected to delay autumn senescence, although conflicting reports exist (Menzel & Fabian, 1999; Penuelas *et al*., 2002; Matsumoto & Ohta, 2003; Delpierre *et al*., 2009; Richardson *et al*., 2010; Vitasse *et al*., 2011). The nature of the control of photoperiod, and photoperiod–temperature interactions, is also not well understood. Nevertheless, these are the drivers used in current models (Richardson *et al*., 2012). The accumulation of cold temperatures, in the form of cold degree-days, has also been recently highlighted as a strong predictor of autumn senescence (Delpierre *et al*., 2009; Dragoni *et al*., 2011; Archetti *et al*., 2013).

The timing of spring has recently been reported to influence the timing of autumn senescence (Fu *et al*., 2014). Using experimental warming, Fu *et al*. (2014) showed that a warming induced earlier spring lead to earlier autumn senescence. Multiple, as yet unresolved, mechanisms could lead to a link between these separate phenological events. For instance, drought is known to affect leaf life span, although the direction of the response is dependent on the magnitude of the drought (Casper *et al*., 2001; Hallik *et al*., 2009; Limousin *et al*., 2010), and an earlier spring could in theory decrease soil water reserves thus leading to an increased prevalence of drought

during summer. Leaf longevity is also modulated by damage during the growing season due to oxidative and biotic stress (Kikuzawa *et al*., 2013), and under the direct genetic control of programmed cell death (Jones & Dangl, 1996; Lam, 2004). Leaf longevity is highly conserved within a species and correlates with a wide range of leaf and plant characteristics (Reich *et al*., 1992; Kikuzawa & Lechowicz, 2011; Kikuzawa *et al*., 2013). The results of Fu *et al*. (2014) were derived primarily from a 5 °C warming experiment, and open questions remain as to whether the relationship is broadly evident in natural and satellite observations.

A widespread link between spring and autumn senescence could greatly limit the response of autumn senescence to future climate change (Hänninen & Tanino, 2011), and potentially invalidate the assumptions of existing autumn phenology models. Here, we use two decades of observations of both spring and autumn phenology of deciduous forest trees at two sites in the northeastern United States (Hubbard Brook Experimental Forest, NH; Harvard Forest, MA), along with concurrent meteorological observations, to examine the relationship between spring phenology and autumn senescence. We combine this analysis with remotely sensed observations from the MODIS Terra and Aqua satellites from 2000 to 2012 and assess whether the patterns detected at the site scale are reproduced over the entire distribution of deciduous dominated forests in the eastern United States. Based on those analyses, we develop a new model of autumn senescence (‘SIAM’–the spring-influenced autumn phenology model) and evaluate its performance for predicting the observed autumn phenology. We then consider the implications of our findings for modeling the response of autumn phenology to future climate change, and the resulting feedbacks to the climate system.

Materials and methods

Hubbard Brook phenological observations

The Hubbard Brook Experimental Forest is located in the northeastern United States, within the White Mountain National Forest in central New Hampshire (43.56°N 71.45°W, 222–1015 m.a.s.l.). The climate is moist temperate with a mean July temperature of 19 °C and mean January temperature of −9 °C. Annual precipitation is 1000 mm and is evenly distributed throughout the year. Phenological observations were collected from three dominant species, American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and yellow birch (*Betula alleghaniensis*) (Richardson *et al*., 2006).

The three co-dominant species were selected for monitoring in 1989 (at nine different locations), with individual trees marked for each species. Each spring and autumn, plots have been visited

approximately weekly, and the developmental stage of each marked tree is recorded. The phenological status of 24 individuals was observed for each species over 24 years (1989–2012).

Here, we define spring on an individual tree basis as the date at which leaves reach 1/2 of final length (database flag ≥3). The autumn transition point is defined as the date at which more than 50% of leaves have changed color (database flag ≥2). Phenology observations are ongoing, and the complete dataset is available online (http://hubbardbrook.org/data/dataset.php?id=51). Concurrent daily meteorological data were also measured (http://www.lternet.edu/sites/hbr).

Harvard Forest phenological observations

The Harvard Forest (42.54°N, 72.18°W, 220–410 m.a.s.l.) is located in the northeastern United States, in central Massachusetts, about 120 km southeast of Hubbard Brook Experimental Forest. The climate is moist temperate, with a mean July temperature of 20 °C and mean January temperature of −7 °C. Mean annual precipitation is 1100 mm and is evenly distributed throughout the year.

Spring and autumn phenology observations have been made at 3- to 7-day intervals on a suite of woody plant species since 1991 (Richardson & Keefe, 2009). Budburst is defined as when 50% of the buds on an individual have recognizable leaves emerging. Weekly observations of percent leaf coloration and percent leaf fall begin in September and continue through complete abscission. Here, we examined the phenological observations of the three species that are tracked at both Hubbard Brook and Harvard Forest (American beech, sugar maple, and yellow birch). The phenological status of 4 individuals was observed for each species over 21 years (1992–2012).

Spring and autumn transitions were defined as the dates at which 95% of leaves have emerged, or 95% of leaves had changed color, respectively, as this has been shown to most closely coincide with other phenological indices for the site (Keenan *et al.*, 2014a). Phenology observations are ongoing, and the complete dataset is available online (http://harvardforest.fas.harvard.edu:8080/exist/xquery/data.xq?id=hf003). Meteorological data used in this study are available at http://harvardforest.fas.harvard.edu/harvard-forest-weather-station.

Remote sensing estimates of phenology

At the regional scale, we analyzed phenology metrics at 500-m spatial resolution for all deciduous forest dominated pixels in the eastern United States. Phenology metrics were

calculated from the enhanced vegetation index (EVI) using 13 years (2000–2012) of MODIS reflectance data (MOD09GA, v005), based on 8-day nadir BRDF-corrected MODIS surface reflectance data (MCD43A4). Quality control filters removed all data that were flagged as cloud, cloud shadow, or cirrus cloud, as indicated in the per-pixel quality assurance data layer, and view angle was constrained to <60°.

Phenological dates were extracted from daily MODIS EVI using a robust smoothing-spline approach (RSM, Keenan *et al*., 2014b). Spring and autumn phenological dates were extracted using the RSM by applying a threshold. For each pixel, spring and autumn thresholds were set at 30% of the mean amplitude for all years for that pixel. For example, the VI spring date was defined as the date at which the smoothed signal first crossed the threshold of mean winter VI +30% of the mean VI amplitude over all years. See Keenan *et al*. (2014b) for further details.

Testing drivers of variability in autumn senescence

The relative influence of key explanatory variables on autumn senescence was tested using partial correlation analysis. The influence of mean autumn temperature (September, October, November) accumulated cold degree-days, and the timing of spring on autumn senescence was examined. Spring and autumn temperatures were not significantly correlated over the examined period.

Models of autumn leaf senescence

We developed a new model of autumn senescence and contrasted its performance and predictions against that of a widely used model based on cold degree-days (Delpierre *et al*., 2009). The Delpierre *et al*. (2009) model predicts autumn senescence using a combination of temperature (*T*) and photoperiod (*P*). Temperature control is modeled via accumulated cold degree-days (*iCDD*), where temperatures below a certain limit (T_b) are accumulated after a certain day length is reached. The model predicts senescence to occur when the accumulated cold temperatures reach a predetermined level (Y_{crit}). Formally, after a set photoperiod (P_{start}) is reached ($P(d) < P_{start}$), cold degree-days are calculated as:

$$CDD(d) = (T_b - T(d)) * \left(\frac{P(d)}{P_{\text{start}}}\right), \; if\, T(d) < T_b$$

$$CDD(d) = 0, \; if\, T(d) \geq T_b \quad (1)$$

where *CDD*(*d*) is the cold degree-day for day, *d*, adjusted for the days photoperiod, *P*(*d*). Cold degree-days are then accumulated as:

$$iCDD(d) = iCDD(d-1) + CDD(d), \quad (2)$$

Senescence (Y_{mod}) is predicted to occur when $iCDD(d) \geq Y_{crit}$. That is,

$$Y_{\mathrm{mod}} = d,\ if\ iCDD(d) \geq Y_{\mathrm{crit}} \quad (3)$$

The model therefore requires three free parameters, T_b, P_{start}, and Y_{crit}. We refer to this model as the CDD model hereafter.

The second model modifies the critical *iCCD* threshold in dependence of spring budburst. In this model, motivated by the linear relationship between spring and autumn dates, Y_{crit} is a linear function of the spring date anomaly:

$$Y_{\mathrm{crit}} = (a + b * S_a) \quad (4)$$

where a, and b are free parameters governing the effect of changes in spring on autumn senescence, and S_a is the observed spring anomaly, or difference between the spring date in the current year and the site-mean spring date. The model therefore requires four free parameters, T_b, P_{start}, a, and b. We refer to this model as the spring-influenced autumn model (SIAM) hereafter.

Both model approaches were optimized to the observations of autumn senescence of the three species common at both sites (American beech, sugar maple, yellow birch) using Markov chain Monte Carlo methods. Parameters estimated were common across the two sites, but varied by species, as suggested by Archetti *et al*. (2013).

Modeling responses of autumn senescence to future warming

To assess model predictions of changes in autumn senescence under future warming, we examined the sensitivity of predicted senescence by running both models with one year of mean daily climatology for Hubbard Brook. We ran multiple simulations, with each one incrementing the mean annual temperature by 0–7 °C by increasing the temperature of each day within the year.

For future autumn senescence estimates, the SIAM model requires estimates of future spring budburst dates. We estimated future budburst dates by taking the mean sensitivity of spring phenology to changes in temperature (−3 d^{-1} °C) across an ensemble of models assessed in a recent study (Migliavacca *et al*., 2012) for the three species included here. As our focus is on quantifying the uncertainty associated with the senescence modeling approach taken, we project model parameter uncertainty forward, but do not incorporate uncertainty associated with the estimated spring dates.

Results

Hubbard Brook observations

Mean spring budburst dates at Hubbard Brook occurred on day of year 143, 141, and 144, with a standard deviation of 5.6, 6.2, and 6.0 days for American beech, sugar maple, and yellow birch, respectively. Mean autumn senescence dates occurred on day of year 284, 279, and 279 with a standard deviation of 3.8, 4.1, and 3.7 days between years. The mean growing season length was 141, 138, and 136 (± 5.0, 6.2, 6.6) days. Variability in the timing of spring budburst was roughly 50% larger than that of autumn.

The timing of autumn senescence was positively correlated (R = 0.68, 0.77, 0.38, partial correlations; P < 0.01, <0.01, 0.09, n = 24 years) with the timing of spring budburst (Fig. 1) at Hubbard Brook for each of American beech, sugar maple, and yellow birch. The slope of the relationship between spring and autumn phenology was well conserved between species, with a one-day earlier spring resulting in a 0.52 ± 0.13 (mean, standard deviation) day earlier autumn (Fig. 1). The relationship was significant at P < 0.01 (Fisher combined probability) across species. The timing of autumn senescence at Hubbard Brook was correlated to a lesser extent to both mean autumn temperature (R = 0.61, 0.56, 0.34, partial correlations; P < 0.01, <0.01, 0.12) and cold degree-days (R = 0.58, 0.54, 0.44, partial correlations; P < 0.01, 0.01, 0.04) for each of American Beech, Sugar Maple, and Yellow Birch, respectively. The results suggest that spring budburst explains more variability in autumn senescence than the examined climate drivers for the three species observed at this site.

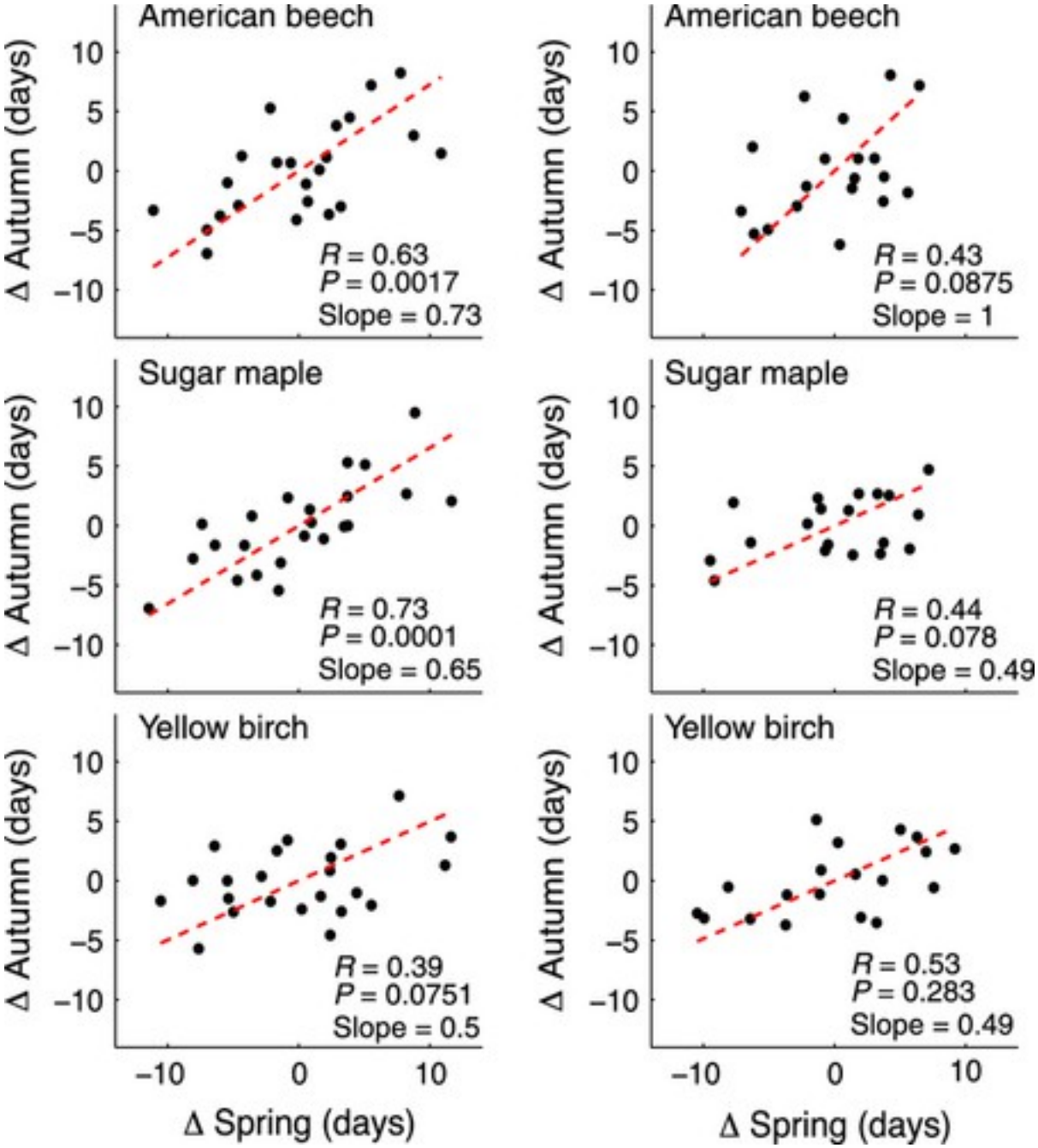

Figure 1

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Ground observations of the relationship between spring budburst and autumn senescence. Partial correlation of spring budburst and autumn senescence obtained for 3 species (American beech, sugar maple, and yellow birch) at the Hubbard Brook Experimental forest (Left, n = 24 years (1989–2012), each point is the average across 24 trees per species) and Harvard Forest (Right, n = 21 years (1992–2012), each point is the average across 4 trees per species).

Harvard Forest observations

Mean spring budburst dates at Harvard Forest occurred on day of year 126, with mean species standard deviation of 6.0 days. Mean autumn senescence dates occurred on day of year 286 with a mean standard deviation of 4.3 days between years. The mean growing season length was 160 (± 6.5) days. As with the Hubbard Brook observations, variability in the timing of spring budburst was roughly 50% larger than that of autumn.

The timing of autumn senescence was positively correlated (R = 0.43, 0.44, 0.53; P = 0.09, 0.08, 0.03, n = 21 years) with the timing of spring budburst at Harvard Forest (Fig. 1b) for each of American beech, sugar maple, and yellow birch. The slope of the relationship between spring and autumn at Harvard Forest was somewhat higher than that observed at Hubbard Brook, with a one-day earlier spring budburst was associated with a 0.66 ± 0.29 (mean, standard deviation) day earlier autumn senescence. Mean autumn temperature was correlated with the timing of autumn senescence (R = 0.39, 0.65, 0.75, P = 0.12, <0.01, <0.01). Accumulated cold degree-days were correlated with autumn senescence with R = 0.55, 0.61, 0.68 (P = 0.07, <0.01, <0.01). The results suggest that autumn temperatures explain slightly more variability in autumn senescence than spring timing across these three species at Harvard Forest.

Spring–autumn relationship at the landscape scale

The pattern of earlier spring onset being associated with earlier autumn senescence, as observed in the ground observations at the two sites in the northeastern United States, was also apparent in MODIS satellite estimates of phenology for the entire Eastern Deciduous Forest region. Autumn dates were positively correlated with spring dates (mean R = 0.43), with a one-day earlier spring leading to a 1.1 day earlier autumn on average (Fig. 2). This suggests that the relationships observed at the two sites in the northeastern United States are representative of processes governing the senescence of a broad range of deciduous species across the eastern United States.

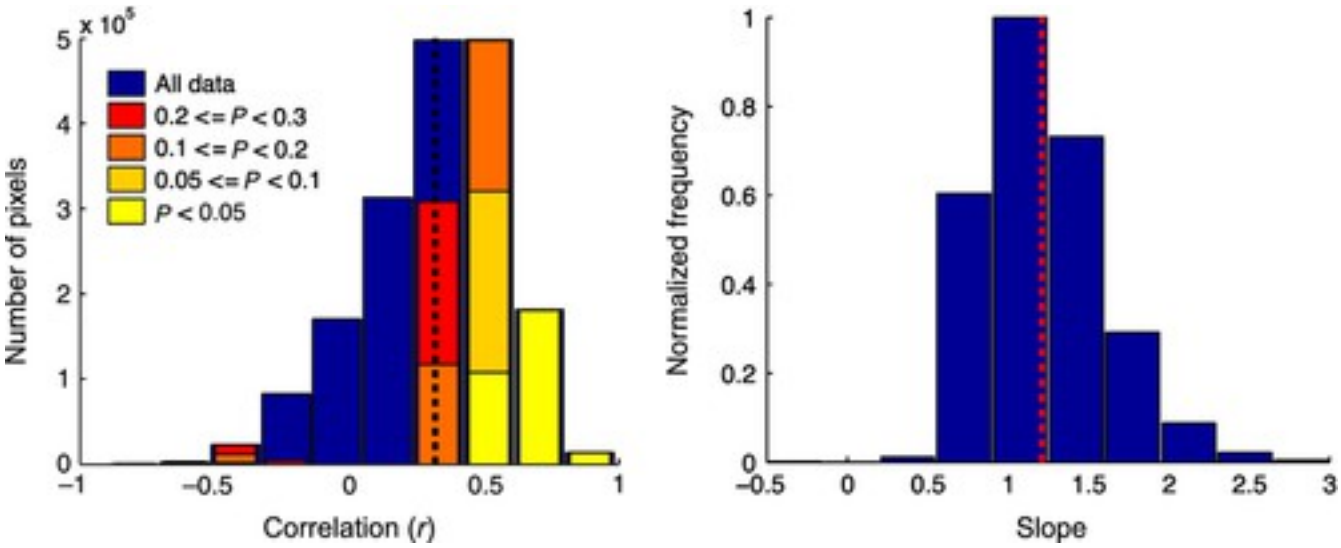

Figure 2

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Satellite observations of the relationship between spring budburst and autumn senescence over the eastern United States. Correlations between MODIS spring and fall phenology for 1.75 million deciduous forest pixels across the eastern United States. Dates were extracted from the enhanced vegetation index (EVI) using a robust smoothed spline method (RSM). Significant values are shown at different levels of significance. The vertical dashed line represents the mean correlation.

Modeling autumn senescence

We developed a new autumn senescence model, which accounts for the influence of spring on autumn senescence (the spring-influenced autumn phenology model, 'SIAM' (see Methods)), based on an existing model that predicts autumn senescence on the basis of photoperiod and cold degree-days [CDD model (Delpierre *et al*., 2009)]. When optimized to the observations at both sites simultaneously, the SIAM model slightly outperformed the CDD model, with species-specific improvements of between 10 and 40% (Table 1). Not surprisingly, the degree of model improvement was in proportion to the species-specific extent to which spring influenced autumn in the observations (Fig. 1). Over all species and sites, the SIAM model gave the best fit to the observations (Fig. 3), with an R^2 of 0.81 ($P < 0.01$).

Table 1. Statistical comparison of modeling approaches

Model	Hubbard Brook		Harvard Forest		Overall	
	RMSE	ME	RMSE	ME	RMSE	ME
American beech						
Null	3.97	0.00	5.66	0.00	4.81	0.00
CDD	3.67	0.15	4.95	0.24	4.31	0.19
SIAM	3.24	0.33	4.78	0.29	4.01	0.31
Sugar maple						
Null	4.23	0.00	3.08	0.00	3.65	0.00
CDD	3.63	0.26	2.02	0.57	2.83	0.42
SIAM	3.20	0.43	2.31	0.44	2.75	0.43
Yellow birch						
Null	3.54	0.00	3.84	0.00	3.69	0.00
CDD	3.09	0.24	3.07	0.36	3.08	0.30

Model	Hubbard Brook		Harvard Forest		Overall	
	RMSE	ME	RMSE	ME	RMSE	ME
SIAM	3.28	0.14	2.77	0.48	3.02	0.31

- A statistical comparison of three models [the null model, the cold degree-day model (Delpierre *et al*., 2009), and the spring-influenced autumn phenology model (SIAM)]. Both the root mean square error (RMSE) and model efficiency (ME) statistic are presented in days for the three species common to both Hubbard Brook and Harvard forest.

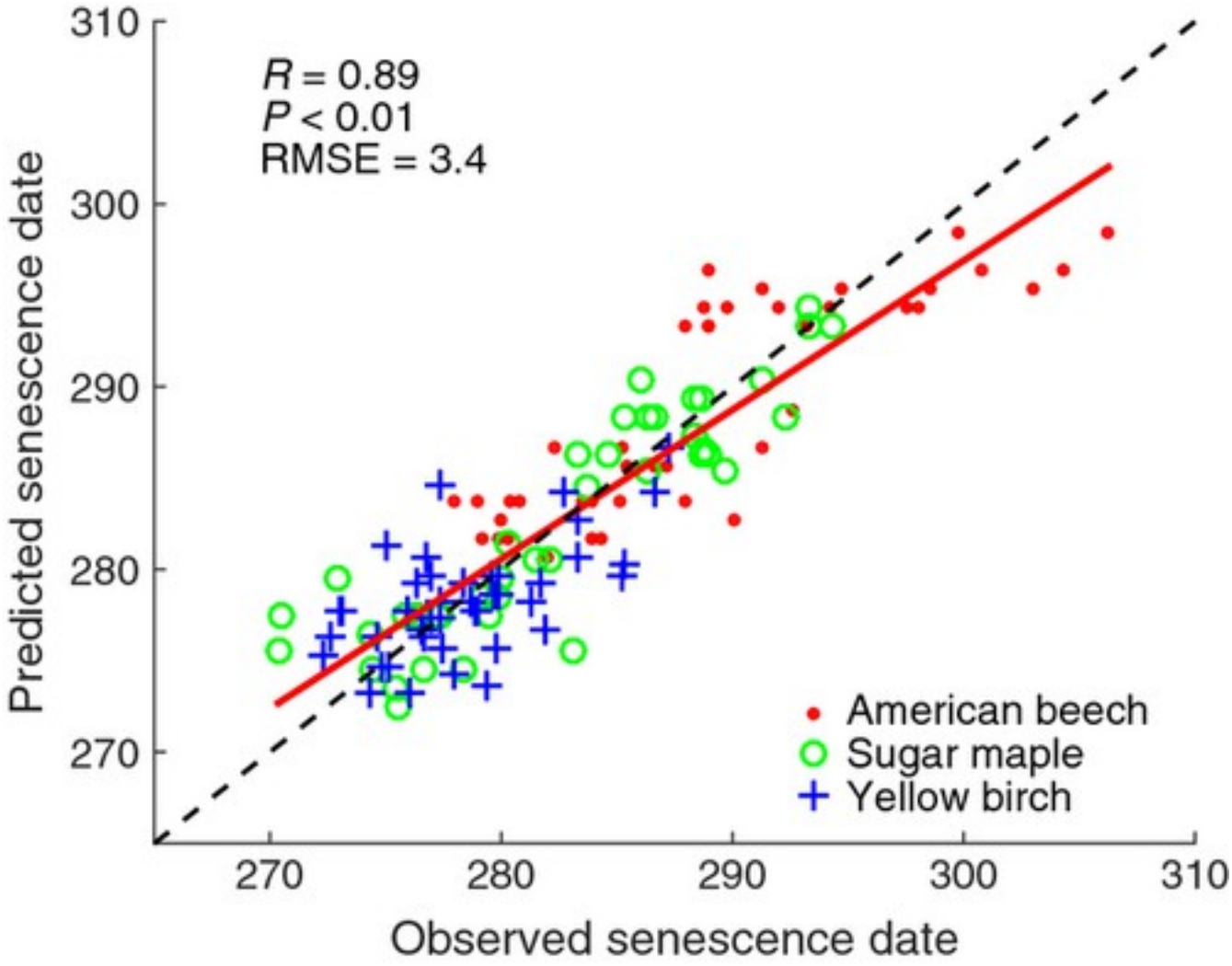

Figure 3

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Modeling spring-influenced autumn senescence. Comparison of observed and predicted autumn senescence dates over the three species and both sites using the spring-influenced cold degree-day model. Red line represents a linear regression.

Modeled response of autumn senescence to future warming

Model projections of the timing of senescence, although comparable during the previous two decades (Table 1), diverged greatly under future climate warming (Fig. 4). The advance of the timing of spring onset under future warming largely dampened the response of autumn senescence to changes in the mean annual temperature in the SIAM model, giving a net predicted delay in mean autumn senescence of between 1 and 5 days by the end of the century (Fig. 4). In comparison, the CDD model, in which autumn senescence is independent of the timing of spring onset, predicted between 7 and 15 days later senescence, depending on the expected extent of future warming.

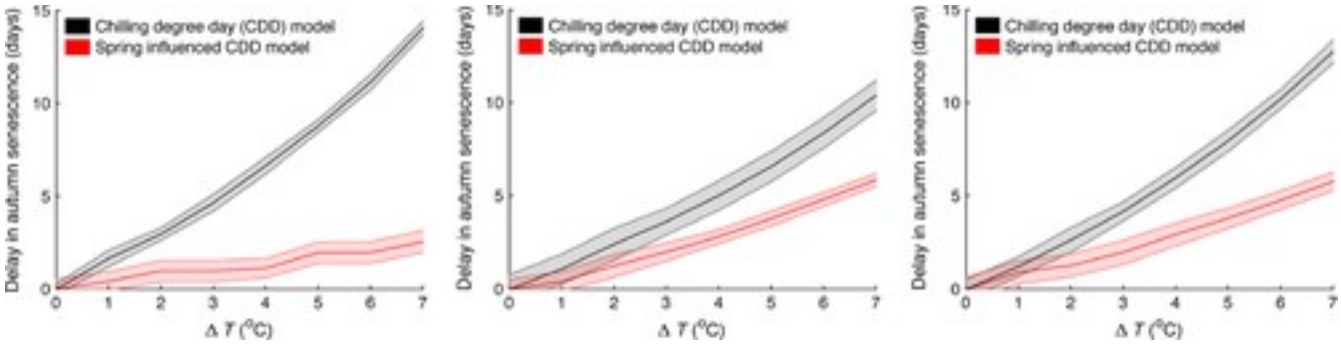

Figure 4

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Implications for modeling the response of autumn senescence to future climate change. Projected autumn phenology change per degree increase in mean annual temperature for American beech (left), sugar maple (middle), and yellow birch (right) using the cold degree-day model with (red) and without (black) the influence of spring. ΔT is the change in mean annual temperature with respect to the period 2001–2010. For reference, a ΔT of 4–5 °C is expected for the study region by 2100 under scenario A1. Shaded areas represent 1 standard deviation of model projections, estimated from the posterior parameter distribution.

Discussion

The timing of autumn senescence in temperate deciduous forests plays a strong role in mediating ecosystem function (Noormets, 2009), the resulting carbon cycling (Keenan *et al*., 2014b), and feedbacks to the climate system (Richardson *et al*., 2013). Despite this, the biotic and abiotic factors that control autumn senescence remain inadequately understood. This greatly hinders the development of accurate autumn senescence models, which are necessary for the projection of ecosystem state and function both for current and future environmental conditions.

We used two multidecade observational records of concurrent spring and autumn temperate forest phenology, and remote sensing estimates of phenology over the entire distribution of deciduous forests in the eastern United States, to examine the influence of spring timing on autumn senescence. As in previous studies, we found a role of temperature in the form of accumulated cold temperatures (Delpierre *et al*., 2009; Dragoni *et al*., 2011; Archetti *et al*., 2013). Confirming experimental results from Fu *et al*. (2014), we report a relationship between the anomaly of timing of spring budburst and that of autumn senescence, both at the scale of the individual organism and the landscape. All other conditions being equal, a one-day earlier spring onset led to approximately a 0.6-day earlier autumn senescence, a value that was consistent across all species/sites examined, and largely replicated across the landscape. This extends previous experimental reports on Quercus robur and Fagus sylvatica (Fu *et al*., 2014), to the deciduous forests of the eastern United States.

Spring is expected to occur earlier under future warming, and indeed recent trends in spring have been reported (Menzel *et al*., 2006, 2008; Cleland *et al*., 2007; Primack *et al*., 2009; Ibáñez *et al*., 2010; Hänninen & Tanino, 2011; Keenan *et al*., 2014b). Trends of later autumn senescence have been less widely observed (but see Dragoni & Rahman, 2012) and are often of lower magnitude than observed trends in spring (Keenan *et al*., 2014b). The link we report here, between spring budburst and autumn senescence, could potentially explain the lack of reports of a strong trend in autumn phenology in response to the warming experienced over the past decades, as the influence of warmer temperatures on autumn senescence would be somewhat offset by the influence of an earlier spring. Such a relationship has large implications, as we show here, for modeling the future response of autumn senescence to climate change.

Current land surface models urgently need to improve their representation of both spring and autumn phenology (Richardson *et al*., 2012). Poor performance stems from a lack of understanding as to the nature of the dominant controls of phenology (Jeong *et al*., 2012; Migliavacca *et al*., 2012; Richardson *et al*., 2013), and an inaccurate characterization of the sensitivity of phenology to those controls currently included in models (Keenan *et al*., 2014b). This lack of understanding is due to both challenges in merging information gleaned at different scales (Hufkens *et al*., 2012a; Klosterman *et al*., 2014), challenges in accurately estimating autumn phenology dates (Garrity *et al*., 2011), and the lack of direct long-term observational and experimental datasets. Using observations from different scales allowed us to identify a generalizable pattern of an influence of spring budburst timing on autumn senescence, which, along with experimental evidence (Fu *et al*., 2014), provides strong support for the development of a new model of autumn senescence.

The spring-influenced autumn model we developed gave a moderately improved performance over a model that did not include the influence of spring on autumn senescence (Delpierre *et al*., 2009) when tested against two decades of observations. The main difference between the two models was observed in their response to future warming. As the climate warms, spring budburst is predicted to advance in temperate deciduous forests (Migliavacca *et al*., 2012). Any connection between spring and autumn senescence would therefore limit the response of autumn senescence to future warming (Hänninen & Tanino, 2011). Projections from the two models tested here diverged greatly under future climate warming, with the spring-influenced model predicting a limited response of autumn senescence to future climate change. It is important to note that this does not imply a growing season of fixed length, as the relationship between spring onset and autumn senescence reported here is not 1 : 1. Our

results suggest that current models that do not include the effects of spring on autumn senescence may overpredict the extension of the growing season by as much as 50% under future warming.

There are multiple mechanisms, both direct and indirect, through which the timing of spring could affect the timing of autumn senescence. Direct mechanisms include leaf structural constraints on longevity (Reich *et al*., 1992), and programmed cell death (Lam, 2004). Indirect mechanisms include the increased probability of drought with an earlier spring (Buermann *et al*., 2013), a related increase in pest attacks and insect outbreaks (Jepsen *et al*., 2011), and occasional leaf damage due to an increased probability of prohibitively cold temperatures post-budburst (Hufkens *et al*., 2012b). Fu *et al*. (2014) also hypothesized that a carbon sink limitation could be induced by an earlier spring, as carbohydrate reserves reach maximum earlier (Herold, 1980; Fatichi *et al*., 2013). The ongoing development of new technologies for phenological observation (Richardson *et al*., 2007; Koch *et al*., 2009; Sonnentag *et al*., 2012) and new techniques for data integration and model testing (Graham *et al*., 2010; Jeong *et al*., 2012; Migliavacca *et al*., 2012; Melaas *et al*., 2013) should help further elucidate the processes responsible for the observed response. Until those processes are understood, our proposed model remains but a hypothesis to be tested with further evidence. It is, however, the hypothesis that is best supported by both the ground and satellite observations presented here, and experimental evidence (Fu *et al*., 2014).

The large constraint imposed on the future extension of the growing season in autumn by warming induced changes in spring stands in contrast to current efforts to model the response of autumn senescence to climate change. Although both modeling approaches examined suggest an extension of the autumn growing season under warmer climate regimes, the results suggest that the potential extension is limited due to the effect of concurrent earlier spring phenology. This has implications for modeling ecosystem function, and associated feedbacks to the climate system such as carbon cycling, changes in albedo, and surface-atmosphere water transport (Richardson *et al*., 2013).

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