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Key Points:
- The spatial variability of green-up days is controlled by climate as well as by physical and chemical properties of forest soil
- Forest floor thickness, the concentration of exchangeable potassium, and soil acidity manifest themselves as controls of surface greening
- Biochemical mechanism linking the forest floor and green-up dates might be instrumental for predicting forest responses to climate warming

Supporting Information:
- Supporting Information S1
- Data Set S1

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A Newly Identified Role of the Deciduous Forest Floor in the Timing of Green-Up

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Abstract Plant phenology studies rarely consider controlling factors other than air temperature. We evaluate here the potential significance of physical and chemical properties of soil (edaphic factors) as additional important controls on phenology. More specifically, we investigate causal connections between satellite-observed green-up dates of small forest watersheds and soil properties in the Adirondack Mountains of New York, USA. Contrary to the findings of previous studies, where edaphic controls of spring phenology were found to be marginal, our analyses show that at least three factors manifest themselves as significant controls of seasonal patterns of variation in vegetated land surfaces observed from remote sensing: (1) thickness of the forest floor, (2) concentration of exchangeable soil potassium, and (3) soil acidity. For example, a thick forest floor appears to delay the onset of green-up. Watersheds with elevated concentrations of potassium are associated with early surface greening. We also found that trees growing in strongly acidified watersheds demonstrate delayed green-up dates. Overall, our work demonstrates that, at the scale of small forest watersheds, edaphic factors can explain a significant percentage of the observed spatial variation in land surface phenology that is comparable to the percentage that can be explained by climatic and landscape factors. We conclude that physical and chemical properties of forest soil play important roles in forest ecosystems as modulators of climatic drivers controlling the rate of spring soil warming and the transition of trees out of winter dormancy.

Plain Language Summary Plant phenology studies usually focus on air temperature. We investigated the potential significance of soil (edaphic) properties as additional important controls on phenology using satellite-observed green-up dates of small forested watersheds and measured soil properties in the Adirondack Mountains of New York, USA. Three factors manifest themselves as significant controls of seasonal patterns of variation in vegetated land surfaces observed from remote sensing: (1) thickness of the forest floor, (2) concentration of exchangeable soil potassium, and (3) soil acidity. A thick forest floor and acidified conditions appear to delay the onset of green-up, whereas watersheds with elevated concentrations of potassium are associated with early surface greening. Our work demonstrates that edaphic factors can explain a significant percentage of the observed spatial variation in land surface phenology and timing of forest green-up that is comparable to the percentage that can be explained by climatic and landscape factors. Further research on how climate change is affecting the start of the growing season will need to incorporate ecosystem factors such as these to understand the response of forests to climate trends.

1. Introduction

Until recently, separating the effects of edaphic factors from other controls of plant phenology has produced equivocal results. In a study of plants growing on former agricultural soil at sea level to a tree line transect in a Fjord district in western Norway, Wielgolaski (2001) observed that the earliest flowering occurred on soils with low pH, whereas high concentrations of exchangeable ions, such as phosphorus (P), calcium (Ca), magnesium (Mg), and potassium (K), often led to delays in seasonal plant development. Nocturnal and diurnal temperatures had consistently strong positive correlations with plant development stages, whereas edaphic factors had statistically significant correlation mostly with earlier phenophases (Wielgolaski, 2001). Edaphic factors, however, demonstrated a strong covariance with temperature (Wielgolaski, 2001), which could not be resolved within the simple multiple regression model used in Wiegolaski's study.

Dahlgren et al. (2007) employed a three-stage statistical model to analyze the flowering time of herbs under a temperate forest canopy. Simple regressions were used to exclude edaphic, climatic, and landscape variables

that were uncorrelated with phenological plant phases. The researchers then used the remaining variables to assess multiple correlations and applied the AIC (Akaike's Information Criterion) to optimize the model. Finally, the Structural Equation Model (SEM) was constructed to test the role of environmental effects on phenology (Dahlgren et al., 2007). The study did not find causative relationships between soil chemistry and phenology, but instead it signified the importance of various local landscape factors measured for each plant, including gaps in tree canopy and slope exposure (Dahlgren et al., 2007). The only exception was the linkage between the early flowering of herbs on southern slopes with potassium-rich soils (Dahlgren et al., 2007). The exact causality in this linkage was not resolved. It is important to note that the SEM typically requires the sample size to be more than 25 times, with a minimum of 10 times, the number of parameters to be estimated (Nachtigall et al., 2003). Therefore, 16 variables (7 environmental and 9 soil factors) would require 160–400 cases. While 5,000 cases are reported in the study, only 25 had independently measured soil properties.

Controlled experiments were conducted by Arend et al. (2015) to evaluate effects of soil acidity on plant phenology. The study used genetically uniform, acclimated European beech (*Fagus sylvatica*) seedlings planted outside a greenhouse on native soils with different pH values. This 2 year experiment revealed that seedlings growing in soils with low pH showed an earlier leaf unfolding date than those planted in soils with higher pH. However, plants growing in low pH soils also had earlier cessation dates and an overall shorter growing season (Arend et al., 2015). Typically, soil acidity at a low pH is regulated mostly by hydrolysis and precipitation of aluminum compounds and under high pH, by precipitation and dissolution of calcium carbonate (Brady & Weil, 2002). The absence of information on concentrations of aluminum and base nutrients and the methodology used for measuring pH (e.g., in water of a salt solution) make interpretation of those findings difficult. It is unclear, for example, if the difference in soil pH was accompanied by changes in concentrations of toxic aluminum species or some other cations and/or soil nutrients, which might have a more direct effect on plant growth.

The overall low number of studies that have assessed effects of edaphic factors on phenology can be explained by the significant complexity of interactions among landscape features, climatic factors, and soil properties. All of these elements are linked by energy, nutrient supply, and water flux, thereby forming a single soil-vegetation-climate system (e.g., Eagleson, 1978). Individual trees are capable of altering soil nutrient concentrations and physical properties in the immediate vicinity within the rooting zone (Waring et al., 2015; Zinke, 1962). At the ecosystem level, various plant-soil feedback mechanisms exist. Mediated by the forest floor, such feedback mechanisms significantly control the relative abundance of tree species in forest communities (Mangan et al., 2010; Ulrich et al., 2014; Xu et al., 2016). Many soil attributes are closely related to landscape features such as slope and aspect, as well as temperature and precipitation, which largely control decomposition rates of soil organic matter, leaching of base cations, and/or soil moisture (Böhner & Selige, 2006; Rezaei & Gilkes, 2005). Thus, an understanding of spatiotemporal patterns in plant phenology cannot be achieved without considering the interactions between plants and their soil environment.

The aim of this study is to assess possible effects of edaphic factors on land surface phenology by using a unique soil data set, remotely sensed satellite data, advanced statistical methods, and physical modeling. Specifically, we tested the hypothesis that edaphic factors are likely to explain a significant percentage of spatial variations in land surface phenology (LSP) in addition to the percentage that can be explained by climatic and landscape factors.

2. Materials and Methods

2.1. Study Area and Scale

We studied spring LSP and soil properties of northern temperate forests in 26 small watersheds ($<$ 1–4 km^2) in the Adirondack region of New York, USA, over an area of about 150 $\times$ 150 km (Figure 1). Watershed boundaries were delineated using a 10 m digital elevation model (https://lta.cr.usgs.gov/NED) (see supporting information). Deciduous trees in the area include sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and the less abundant red maple (*Acer rubrum*) and yellow birch (*Betula alleghaniensis*). The mixed forest also contains coniferous species, including red spruce (*Picea rubens*) and eastern white pine (*Pinus strobus*). Canopy tree ages range from about 90 to 150 years (Bishop et al., 2015). Overall, the Adirondack region is characterized by significant variations in soil physical and chemical properties. This was one of the North American regions most impacted by atmospheric acidic deposition of sulfur and

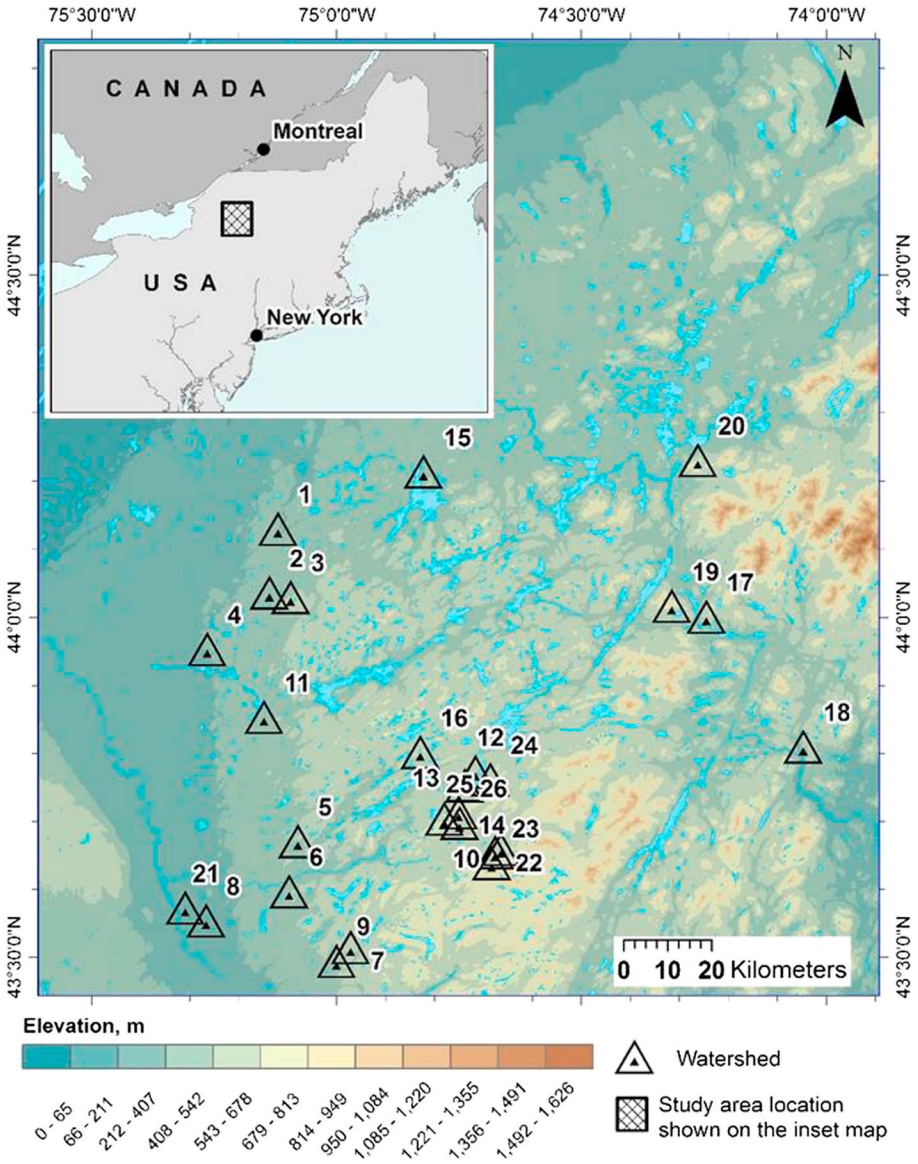


Figure 1. Locations of 26 study watersheds.

nitrogen (N) in the 1970s and 1980s. The region is now showing partial recovery in response to reduced levels of acidic deposition (Lawrence et al., 2015), while at the same time experiencing climate warming (Beier et al., 2012).

While no broadly accepted methodological approach is currently available for defining the temporal scale for relating soil data to climatic or biological variables, a typical turnover time of a deciduous forest floor in northeastern U.S. varies from 4 to about 9–16 years (Vogt et al., 1995). Therefore, we averaged all remotely sensed and climatic variables over the entire 14 year period of Moderate Resolution Imaging Spectroradiometer (MODIS) observations, from 2001 to 2014. In addition to temporal averaging, phenological and soil variables were also averaged within each watershed. Our reasons for performing analysis by watersheds rather than by soil plot are described below.

First, to analyze the data by plot rather than watershed would be counter to the study design and would exacerbate pseudoreplication problems. Soil data were collected during studies focused on developing a better understanding of complex interactions between soil and water chemistry including recovery of soil after several decades of acidification. Stream chemistry collected at the watershed pour point represents

an integration of biogeochemical processes (including edaphic processes) within the study watersheds. Therefore, one of the variables we used in this study characterizes the overall state of watershed acidification (ACID) and was derived via a comparison of soil and stream water chemistry (Lawrence, McDonnell et al., 2017). The soil plots were selected to fall within these selected watersheds to include a hardwood forest that was relatively consistent in composition across plots. Based on this design, the plots within watersheds could not be considered independent.

Second, the small plot size is incompatible with the scale of the available climate data. Each soil plot is about 0.1 ha in area. The climate data, in turn, have a resolution of 1 × 1 km. Therefore, in this paper we relate climate data to vegetation and soil data at the scale of a watershed (1–4 km^2). This scale is adequate for comparing climatic data with averaged watershed-wide soil and satellite variables. Station-based, climatological analysis of climatic variables, and especially temperature, demonstrates that when averaged over more than 10 years these metrics do not change much at the spatial scale from a few to tens of kilometers (e.g., Vinnikov et al., 2011).

Third, plants and soil form feedback mechanisms that influence relative abundance of tree species (Mangan et al., 2010; Ulrich et al., 2014; Xu et al., 2016), which in turn could affect the timing of phenological transitions when averaged over the entire watershed. Coniferous trees (e.g., spruce) typically reach a photosynthesis compensation point and start to increase chlorophyll concentration in needles early in the season (e.g., March–April) (Grossnickle, 2000), whereas deciduous trees in the northeastern U.S. will visibly change canopy reflectance only after a leaf opening event (typically in mid-May) (Richardson et al., 2006). Therefore, from the perspective of statistical modeling, watersheds with some percentage of coniferous forest should green-up earlier in spring than watersheds without coniferous forest. This effect can only be seen at the scale of an ecosystem or watershed, but not at the scale of individual soil plots.

2.2. Dependent and Independent Variables

Below is a brief description of the variables used in this study. The complete list of all variables is provided in Table S1 (supporting information).

2.2.1. Start of Season

Start of Season (SoS) dates (dependent variable) were estimated via the remote sensing approach, also referred to as land surface phenology (De Beurs & Henebry, 2004; Hanes et al., 2014; Schwartz, 2013; White et al., 2009). We used phenology data for the period of 2001–2014 (provided by the U.S. Geological Survey (USGS), http://phenology.cr.usgs.gov/), which recorded the first day with consistent canopy greening as an indication of SoS. The SoS was estimated from the time series of 250 m Normalized Difference Vegetation Index (NDVI) from the Moderate Resolution Imaging Spectroradiometer (MODIS) smoothed using the time-weighted least squares linear regression. The SoS is identified as the first day of significant increase in the rate of change in NDVI. Although LSP does not reflect the phenology of individual trees, it has proven to be useful in explaining general changes in biological activity at watershed scales (Hanes et al., 2014). Watershed-scale phenological transitions could be influenced by climatic, landscape, and edaphic factors and by plant-soil feedback mechanisms.

2.2.2. Climate

Study watersheds were limited to elevations suitable for northern hardwood forests (less than approximately 760 m). Gridded daily air temperature and precipitation data were obtained from the DAYMET data set at 1 × 1 km resolution (Thornton et al., 2015; Thornton et al., 1997). Recent analyses of temporal trends of satellite phenology in the Northern Hemisphere, as well as the large number of ground-based phenological monitoring studies, indicate the importance of daytime maximum, rather than nighttime, temperatures in regulating the date of spring green-up (Piao et al., 2014). In our analysis, we use daytime monthly average maximum temperatures and monthly precipitation values, represented by a total of 24 variables.

2.2.3. Landscape

Landscape variables were derived by analyzing topographic characteristics using the 10 m DEM and Environmental Systems Research Institute ArcGIS extensions for viewshed analysis and estimating solar radiation. We considered the average elevation of a watershed above sea level, slope, aspect, percentage of flat surface in the entire watershed, photoperiod, and total (direct and diffuse) solar radiation (Rich et al., 1994). Cloud cover was assumed constant and equal to 0.5 in the estimation of total radiation.

2.2.4. Land Cover

The categorical variable land cover (*L*) at a 250 m spatial resolution (supporting information Table S2) is based on the relative abundance of tree species in each watershed. Of the 26 study watersheds, 13 were covered entirely by deciduous broadleaf species, 7 by largely deciduous forests with some mixed forest, 4 by largely mixed forest with some deciduous forest, and 2 by mixed forests throughout (Table S2). Studies at another site in the northeastern U.S. (Hubbard Brook Experimental Forest, New Hampshire) demonstrated that the three most abundant broadleaf species in our watersheds, sugar maple, American beech, and yellow birch, have statistically similar phenological patterns (Richardson et al., 2006). The introduction of the new categorical variable (*L*) was mainly important to account for the percentage of coniferous species (Table S2). In addition, net primary productivity (NPP), the standard MODIS product (MOD17A3) available at 1 km resolution from the NASA's Earth Observing System Data and Information System website (http://reverb.echo.nasa.gov/) was used and was also averaged for each watershed (Table S3).

2.2.5. Soil

Forest floor samples were collected during June–September of 2004 and 2009. Forest floor, the surface organic soil layer, is composed of three horizons: *Oi* (relatively fresh litter), *Oe* (partially decomposed litter) and *Oa* (decomposed organic matter in various stages of humification). In these soils, Oe and Oa horizons hold the majority of fine roots within the soil profile. These organic soil horizons have several well-established roles in forest ecosystems, including regulation of soil respiration and evapotranspiration, storage and release of nutrients, and provision of habitat for microbial fauna, insects, and other organisms (Dueser & Shugart, 1978; Gundersen et al., 1998).

We focused on the Oa horizon because these soils hold a substantial fraction of the organic matter contained within the forest floor (somewhat less than half to greater than half depending on the location). These soils play key roles in controlling soil moisture and nutrient availability for trees, and more clearly express site-to-site differences in forest floor characteristics (including thickness) than Oi and Oe, which are less decomposed and more strongly retain the characteristics of litter. The Oa horizon was measured for thickness and sampled for chemical analyses at 10–15 locations within each watershed using a pin block as described in Sullivan et al. (2013) or by horizontal excavation from a soil pit face.

Sample processing and chemical analyses were conducted at the USGS New York Water Science Center Laboratory (Troy, NY). Samples were passed through a 2 mm sieve and analyzed for moisture content (oven drying at 65°C); exchangeable Ca^{2+}, Mg^{2+}, Na^{+}, and K^{+} (unbuffered 1 M NH_4Cl vacuum extraction); and pH (0.01 M $CaCl_2$ slurry; deionized water slurry) following standard U.S. EPA methods (Blume, 1990). Loss on ignition (LOI) was measured by combustion of soil samples in a muffle furnace. Total concentrations of C and N were estimated by a CN analyzer (Blume, 1990). Exchangeable Al was determined by 1 M KCl batch extraction and measurement by an inductively coupled plasma mass spectrometer. Exchangeable acidity was determined by 1 M KCl batch extraction and measurement was done by titration (Thomas, 1982). Exchangeable H^{+} was calculated by subtracting exchangeable Al from exchangeable acidity. Soil data used in this paper are available in Lawrence, Sullivan, et al. (2017).

In addition to these conventional characteristics of soil acidity, we also included a variable (termed ACID) that reflected whether or not acidic deposition was causing mobilization of soil aluminum. This characteristic was derived through a comparison of soil and stream samples collected from the same watersheds (Lawrence, McDonnell et al., 2017). ACID is a categorical variable with three possible values: acidified (ACID(A)), buffered (ACID(B)), and neutral (ACID(N)). In acidified watersheds, mobilization of aluminum within the soil is reflected by measureable inorganic monomeric Al in surface waters (Lawrence et al., 2007), whereas in watersheds with sufficient acid buffering capacity, this form of Al is not mobilized. The mobilization of Al within soils from acidic deposition is a threshold process that occurs when base saturation decreases below about 17% (Lawrence, McDonnell et al., 2017). Bulk Density (BD) was calculated from LOI by the method of Federer et al., (1993) for northeastern forest soils. BD data were used to estimate the thermal diffusion coefficient for calculating the delay in penetration of the spring heat wave into the forest floor (see below).

2.3. Statistical Analysis

2.3.1. Variable Selection

In this study, we used partial least squares regression (PLSR), which is also referred to as projection on latent structure regression. This statistical modeling approach is designed to work with large numbers of collinear

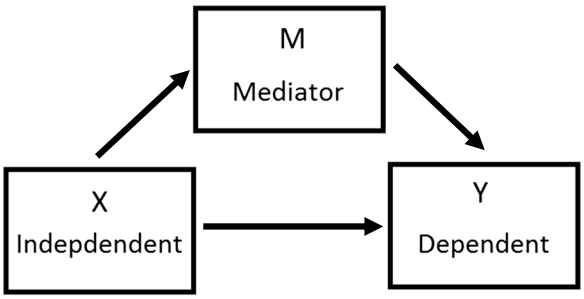


Figure 2. Regression-based mediation model for detection of an indirect effect within selected VIP variables in the PLSR model. The paths $X \rightarrow Y$, $X \rightarrow M$, and $M \rightarrow Y$ represent zero-degree relationships, while the path $X \rightarrow M \rightarrow Y$ indicates multiple regression between SoS (Y) and independent variables. Some variables could play roles as mediators (M).

variables (Abdi, 2010). The Variance Importance in Projection (VIP) criterion was used to identify variables with a significant contribution to the spatial variability of SoS dates in the PLSR. The method of PLSR includes an analysis of degrees of freedom, algorithms for model cross validation, and information criteria for variable selection. The VIP metric is a weighted sum of squares of the PLSR weights, which takes into account the explained variance of each PLSR dimension (principal component). Therefore, VIP provides the explanatory power of predictor variables with respect to the response variable (Akarachantachote et al., 2014). The "greater than one" rule is generally used as a criterion for variable selection because the average of squared VIP scores is equal to 1. Sometimes, however, the VIP $>$ 0.7–0.8 rule can lead to successful selection of variables (Eriksson et al., 2013). More importantly, application of the VIP criterion allows one to retain all the variables that provide an increase in the predictive ability of the model (Indahl et al., 2009).

The choice of VIP is not one of convenience but necessity. Application of conventional regression criteria to the pool of variables with collinearities unavoidably leads to the loss of information. For example, the selection of variables based on AIC or R^2 in general stepwise regression automatically causes the loss of contributions from variables that are collinear with selected variables. However, these variables might be linked to the dependent variable by some real physical or biochemical mechanism. In the PLSR model, collinearity is not an obstacle and all variables selected via the VIP contribute to the variability of statistically significant principal components. An example could be the effect of temperature and elevation on phenology. Temperature decreases with elevation because of the basic adiabatic law that results in a close collinearity with elevation. In rugged terrain, elevation might have some additional direct mechanisms (e.g., change in the length of photoperiod regulated by shadows of nearby mountains) that may affect phenology. If we were to use an AIC or R^2 criterion, then one of these two variables must be abandoned because the correlation matrix would be ill constructed due to the close correlation between temperature and elevation. The VIP criterion in a PLSR allows us to keep both of these factors and estimate their relative contributions into different principal components. In this work, VIP scores were calculated using the Nonlinear Iterative Partial Least Squares (NIPALS) algorithm with v-fold cross validation (v = 7). NIPALS produces accurate VIP estimates compared to other methods (Wold, 1975).

The VIP criterion, however, does not always allow the selection of variables with direct physical or biochemical effects on the dependent variable. Interannual anomalies of spring temperature often correlate with anomalies for other months. For example, spring and summer temperatures can both be below normal during cold years, resulting in high correlations between mean temperatures of different months. In most cases, the temperature before the onset of leaf emergence matters the most for the spring phenology during a given year. However, temperature, and possibly the precipitation of other months, could be highly correlated with spring phenophases due to their covariation with spring weather. In this work we are trying to identify causal connections between edaphic factors and phenological transitions. Therefore, it is important, first of all, to detect the variables that have the strongest direct links to SoS.

2.3.2. Test on Mediation and Significance of Indirect Effect in the PLRS Model

Mediation is the potential causal chain whereby one variable affects another, which, in turn, controls the third variable (MacKinnon et al., 2012). We evaluated possible mediation and indirect effects using methods proposed by Judd and Kenny (1981) and Baron and Kenny (1986). The first step was to establish if zero-order relationships among the variables exist (paths $X \rightarrow Y$, $X \rightarrow M$, $M \rightarrow Y$) (Figure 2). If any of these paths were found to be insignificant, we concluded that mediation did not exist. If all paths were significant, the second step evaluated the significance of multiple regression in the path $X \rightarrow M \rightarrow Y$. Full mediation was supported when the coefficient for partial regression of X was not significant, while M was still significant. Partial mediation was discovered when both X and M had significant multiple regression coefficients. Because these first two steps could still miss true mediation effects (MacKinnon et al., 2012), a third step was also necessary. This involved the calculation of the significance of possible indirect effects as proposed by Judd and Kenny (1981). We calculated the indirect effect as the difference between two regression coefficients—the simple regression coefficient of X in the $X \rightarrow Y$ path and the partial regression of X in the $X \rightarrow M \rightarrow Y$ path (Figure 2).

The significance of the difference between these two regression coefficients was calculated via bootstrapping of standard errors (Shrout & Bolger, 2002).

The final set of independent variables used in the PLSR model was obtained after rejecting fully mediated variables. This resulting model was used to estimate the role of edaphic factors in controlling spatial variability of SoS dates. We used the STATISTICA 13.2 software package (statsoft.com) to perform all PLSR analyses.

2.3.3. Addressing the Causality Between Phenology and Forest Floor Properties

We started this analysis under an assumption that edaphic variables influenced the spatial variability of SoS dates, but not vice versa. One could also hypothesize, however, that instead of soil affecting plant phenophases, plant phenology could act as a forming factor of soil characteristics. An early SoS, for example, could mean a longer period without snow and prolonged rainfall resulting in greater soil leaching, which might lead to an alteration of soil exchangeable chemistry. This particular example, however, is likely to be less important in the Adirondack region where acidic deposition has strongly affected soils (Johnson et al., 2008; Warby et al., 2009) and the spatial patterns of soil base leaching are consistent with patterns of acidic deposition levels (Sullivan et al., 2013). Nevertheless, we cannot completely dismiss this general potential problem of causality in phenology-soil interactions and therefore tackle this problem via two independent approaches.

1. Measuring the potential mediation of variability in edaphic factors (*Y*) by SoS considered in our PLSR framework as a possible mediator (*M*) with other variables considered independent (*X*) (Figure 2). In essence, we were testing if correlations between SoS and edaphic factors selected for the model were stronger than those between these edaphic factors and other variables.
2. Constructing a physical, process-based model (below) to assess the proposed mechanism to strengthen the evidence of causality.

If the first test yields no mediation, we can state that edaphic factors with links to SoS control watershed phenology. If strong mediation by SoS is found, we conclude that SoS might control edaphic factors. A third option is of course also possible, namely a scenario where SoS controls some factors that were left outside our analysis. It is possible that these unidentified factors might control measured soil properties. We do believe, however, that our data are quite comprehensive and cover the most important variables relevant to edaphic controls of plant phenology.

2.3.4. Uncertainty Analysis

We used estimates of spatial variability of soil measurements as a possible source of error. At each watershed, we estimated the standard deviation of soil metrics within the entire population of soil sampling sites. Methodological errors of soil analysis were not accounted for in our calculations because they were an order of magnitude smaller than errors related to spatial variability. For watersheds where samples were collected in both 2004 and 2009, standard deviations were divided by the square root of 2 to account for two independent measurements of the same variables (Table S4).

Uncertainties in remotely sensed data were assessed based on analyses of spatial and temporal variability. Errors were estimated as standard deviations of all watershed pixels over the period of 2001–2014 divided by the square root of 14, the number of complete observation years (Table S4).

2.3.5. Monte Carlo Modeling: Testing Adequacy of Sample Size

To test if the sample size was adequate for this given model, a bootstrapping technique was applied by introducing random distortions into the dependent variable and observing the model response. If such an experiment demonstrates the relative stability of the explanatory power of the model, based on R^2, then we can conclude that the sample size was adequate for construction of the given model. In this work, we employed the rnorm function from the stats package in R. We generated random realization of SoS values for each watershed with mean equals SoS and standard deviation equals σ, where SoS is the estimated value in section 2.2.1 and σ is the standard deviation of watershed-average SoS estimate (see Table S5). Finally, we compared modeled R^2 estimates with R^2 derived through PLSR analysis.

2.4. Process-Based Modeling

Here we use a simple thermal diffusion model to address causality and estimate the magnitude of potential effects of forest floor thickness identified as the independent control of watershed phenology (below). We hypothesize that this linkage is a manifestation of the process of fine root recovery after winter dormancy.

The propagation of a spring heat wave through the soil can be described well by the application of mathematical models of thermal diffusion (J.R.P., 1963). For steady state model conditions, the delay in temperature increase (Δt) between the surface and some soil depth h can be described as

$$\Delta t = h/\omega d \tag{1}$$

where ω is the angular frequency of surface temperature and d is the damping depth (Jury & Horton, 2004), which can be calculated as a function of ω and the coefficient of thermal diffusivity (λ):

$$d = \sqrt{\frac{2\lambda}{\omega}} = \sqrt{\frac{\lambda\tau}{\pi}} \tag{2}$$

where τ is the time period (1 year). The λ values of the forest floor depend on bulk density and the proportion of organic matter relative to water and air. We calculated λ in accordance with the approach used by J.R.P. (1963) (Table 3). This model is applicable to the gradual and consistent warming of a forest floor during spring.

3. Results

3.1. Spatial and Temporal Variability of SoS

Estimates of statistical significance of temporal trends in SoS in individual watersheds can be found in the supporting information (Table S6). None of the watersheds showed a statistically significant ($p < 0.1$) temporal trend in SoS dates. Perhaps, the time interval of the available MODIS data (2001–2014) was too short to detect changes in SoS dates for the Adirondack Mountains. However, SoS values averaged over time did exhibit a distinct mosaic of spatial variability among watersheds. Some watersheds demonstrated a consistently early SoS, whereas some others demonstrated relatively late SoS dates. These watershed-average SoS dates expressed as day of year after 1 January, ranged from 97.8 ± 2.7 to 115.4 ± 2.4 (Table S6). The following presents results of the analysis of relationships between watershed-average SoS and spatial patterns of climatic, landscape, and edaphic variables.

3.2. Results of Statistical Analysis

We found 30 variables that had VIP > 1. Most were climatic, including the 12 variables representing daytime monthly averaged temperature and 7 that were monthly precipitation measurements (Table S1). The top four variables in this list are total radiation, photoperiod, elevation above sea level, and the percentage of flat surface within a watershed area. Edaphic factors with a VIP > 1 include ACID, thickness of the Oa horizon (h), concentration of exchangeable H^+, and concentration of exchangeable K^+. For the concentration of exchangeable aluminum (Al^{3+}), the VIP = 0.9, and all other edaphic variables had VIP values below 0.7 (Table S1).

Analysis of mediation revealed that a single climatic factor—April daytime average monthly temperature (T_Apr)—fully mediates (see section 2) all other climatic variables (Table S5). In other words, maximum daytime temperature describes all the significant spatial variability in SoS when it is related to local climatic conditions. Of the remaining variables with VIP values that exceed or approach 1.0, the concentration of exchangeable Al^{3+} was found to be fully mediated by T_Apr. The T_Apr variable, however, does not mediate the effect of the four remaining edaphic factors (ACID, h, exchangeable K^+, exchangeable H^+) on SoS (Table S5).

As expected, T_Apr shows a strong linkage to elevation above sea level. Simple correlation between elevation and SoS results in a slope of 2.1 ± 0.9 days per 100 m, which is consistent with the Hopkins Law of Bioclimatics (Hopkins, 1920). At the same time, T_Apr does not fully mediate the effect of elevation on SoS. The remaining top landscape variables with the highest VIP (Table S1) are also not mediated by T_Apr (Table S5).

The resulting PLSR model (Tables 1 and 2) has two significant principal components and includes 12 independent variables. In addition to the four edaphic variables mentioned above, the model includes the following: elevation above sea level, land cover type, total radiation, photoperiod, aspect, percentage of flat area within watershed, net primary productivity, and T_Apr. These 12 variables with two principal components describe about 82% of the spatial variation in the SoS (Table 1). The n:v ratio of cases (n = 26) to variables (v = 12) is 2.2, which is smaller than the traditionally recommended factor and principal component analysis ratio of 5 and

Table 1
Partial Least Squares Regression (PLSR) Model Analysis Summary

HIN	R2X	R2X (cumul.)	Eigenvalues	R2Y	R2Y(cumul.)	Q2
1	0.18	0.18	3.40	0.67	0.67	0.40
2	0.07	0.26	1.11	0.15	0.82	−0.77

Note. An estimated 82.2% of the sum of squares of the dependent variables has been explained by all the extracted components.

higher (Gana et al., 2005). We should keep in mind that each of our cases represents an average of 2 to 5 soil plots which, in turn, consist of several soil profiles in each soil plot.

In many studies, stable models have been found with extremely small ($n{:}v < 1$) sample sizes (Preacher & MacCallum, 2002). The conventional wisdom is that a sufficient sample size depends on the quality and type of data, and under favorable conditions even a small number of samples might suffice. In our work, we tested the adequacy of sample size by employing Monte Carlo modeling. Running the PLSR model for 120 iterations with varying sets of SoS values ($n{:}v = 10$) resulted in an R^2 value of 81% ± 3% and an average number of principal components of 2.3 ± 0.4. The similarity between modeled and actual R^2 (Table 1) confirms the relative stability of the 12-variable PLSR model, thereby suggesting the adequacy of the sample size.

We further tested the sensitivity of the PLSR model by (a) removing all four edaphic variables from the model, and (b) leaving only edaphic variables and removing climatic and landscape factors. We found that the model without edaphic factors loses one principal component and can describe about 57% of SoS spatial variability ($n{:}v = 3.3$). Removing all landscape and climatic variables and leaving only four edaphic factors reduces R^2 to 48% and leaves only one significant principal component ($n{:}v = 6.5$). This test demonstrates that the four edaphic factors in the final PLSR model control from 25% to 48% of SoS variability and, apart from climatic and landscape factors, provide an additional degree of freedom.

Analysis of PLSR loading coefficients (Table 2) demonstrate that four edaphic factors—ACID, exchangeable H^+, exchangeable K^+, and *h*—all have at least one loading coefficient greater than 0.4. Loading coefficients greater than 0.4 are usually considered as factor loading cutoffs (Stevens, 2009). The sign of a loading coefficient reflects the direction of the contribution to a given principal component. Three of the four edaphic factors have positive loading coefficients. Thus, an increase in the value of one of these variables causes an increase in the watershed-average SoS date (a delay of spring). The two noticeable exceptions were the significant negative loading coefficients in the second principal component, exchangeable K^+ and ACID(B). Here we were able to separate the effect of higher concentrations of exchangeable K^+ on SoS from the effect of aspect. Table 2 shows that a southerly aspect (AS) and exchangeable K^+ both have a significant negative loading coefficient in the second principal component, whereas AS has another significant loading coefficient into the first principal component. Table 2 shows that watersheds with well-buffered soils (ACID(B)) are characterized by early SoS (significant negative loading coefficients), whereas strongly acidified watersheds with elevated levels of dissolved aluminum in stream water (ACID(A)) are characterized by a delay in the SoS date (significant positive loading coefficients).

Table 2
Loading Coefficients of Variables for Two Principal Components in the PLSR Model

	Loading coefficients	
Variable	Component 1	Component 2
NPP	**−0.65**	−0.14
Land cover (LD)	**−0.62**	−0.10
Percent of flat surface within watershed	**−0.60**	0.37
T_Apr	**−0.58**	0.19
Aspect (S)	**−0.57**	0.20
Photoperiod	**−0.49**	0.21
ACID(B)	**−0.42**	**−0.56**
K^+	−0.30	**−0.44**
H^+	−0.26	**0.67**
Acid(N)	−0.11	−0.09
Land cover (LC)	−0.09	**0.42**
Land cover (LB)	−0.04	0.33
Aspect (SW)	0.15	0.20
Aspect (W)	0.20	−0.31
Aspect (SE)	0.33	−0.21
h	**0.41**	**0.46**
Land cover (LA)	**0.43**	**−0.52**
Total radiation	**0.46**	**0.44**
ACID(A)	**0.46**	**0.58**
Elevation above sea level	**0.65**	−0.13

Note. Aspect and land cover variables are categorical with four values each (Tables S2 and S3). The ACID variable has three categories: acidified (A), buffered (B), and neutral (N) (Table S3). Boldface indicates statistically significant loading coefficients (see text for details). Abbreviations are as follows: NPP (net primary productivity), T_Apr (monthly averaged daily temperature), K^+ (exchangeable K^+), and H^+ (exchangeable H^+).

The first principal component (which explains 67% of SoS variability, Table 1) demonstrated moderately strong correlations with several factors (Table 2). Elevation above sea level has the highest positive loading coefficient of 0.65, whereas average watershed NPP had the highest negative loading coefficient of −0.65. Therefore, the two primary controls of watershed phenology in this analysis are watershed elevation and NPP. An increase in elevation causes delay, while an increase in NPP creates a "spring forward" for SoS dates. Other important controls of the first principal component are landscape factors such as photoperiod, percent of flat area within watershed, total radiation, southern slope exposure, and April daytime temperature.

The second principal component, which describes about 15% of SoS spatial variability, is mostly controlled by edaphic factors. The similar loading coefficients of ACID(A) and ACID(B) with opposite signs suggest the

Table 3
Bulk Density (BD) of Forest Floor Calculated From Loss on Ignition Data as Described by Federer et al. (1993) and Thermal Diffusion Coefficient (λ) Calculated According to J.R.P (1963) for Three Soil Moisture Levels: 0%, 50%, and 100%.

		$\lambda \times 10^{-7}$ (m^2 s^{-1})		
Watershed#	BD (g cm^{-3})	0%	50%	100%
1	0.16	0.34	0.91	0.62
2	0.17	0.35	0.92	0.63
3	0.17	0.35	0.92	0.63
4	0.14	0.32	0.89	0.6
5	0.18	0.35	0.92	0.64
6	0.14	0.32	0.89	0.61
7	0.15	0.33	0.9	0.62
8	0.15	0.32	0.9	0.61
9	0.18	0.35	0.93	0.64
10	0.17	0.35	0.92	0.63
11	0.18	0.35	0.92	0.64
12	0.15	0.32	0.9	0.61
13	0.16	0.33	0.9	0.62
14	0.16	0.34	0.91	0.62
15	0.16	0.33	0.9	0.62
16	0.16	0.33	0.9	0.62
17	0.17	0.34	0.91	0.63
18	0.14	0.31	0.88	0.6
19	0.17	0.34	0.92	0.63
20	0.17	0.35	0.92	0.64
21	0.07	0.25	0.82	0.53
22	0.15	0.33	0.9	0.61
23	0.12	0.3	0.87	0.58
24	0.17	0.35	0.92	0.63
25	0.16	0.34	0.91	0.63
26	0.14	0.31	0.88	0.6

influence of a distinct threshold for aluminum mobilization. Therefore, we can characterize the effect of this variable on SoS dates either by concluding that watershed acidification delays SoS dates or that SoS dates are typically early at watersheds with well-buffered soils.

Causality test #1 (see section 2) showed no significant indirect effect of SoS on three edaphic variables (exchangeable K^+, exchangeable H^+, and *h*; Table 4). We did, however, exclude the categorical variable ACID from this test because ACID does not have any significant zero-order relations with SoS and therefore cannot be mediated by SoS (e.g., Baron & Kenny, 1986). The significance of all zero-order relations among variables used in this analysis and exchangeable K^+, exchangeable H^+, and *h* is shown in Table S7. This table demonstrates that these three variables have significant correlations only with total Exchangeable Acidity (EXA). Therefore, in our estimates of the indirect effect of SoS on these variables, we compared the effect of SoS with the effect of EXA. Overall, the results given in Table 4 demonstrate that the correlations of three edaphic factors with EXA are much stronger than with SoS. Therefore, SoS is unlikely to control these three edaphic variables. This suggests that its indirect effect on edaphic factors is not significant (Table 4). We conclude that in this PLSR model none of the edaphic factors can be controlled by SoS. Rather, edaphic variables (ACID, exchangeable H^+, exchangeable K^+, and *h*) control SoS through their contribution to two principal components, especially through component 2 (see above).

3.3. Results of Processed-Based Modeling

Test #2 of causality was provided by the thermal diffusion model (equations (1) and (2)). Calculations of the delay between atmospheric and soil temperatures during spring warming were conducted for two extreme cases of soil moisture, 0% and 100%, at an average soil bulk density of 0.16 (g cm^{-3}; Table 3). For comparison, we demonstrated 95% confidence intervals of estimates of SoS delay calculated as a slope of the final PLSR model as related to changes in the thickness of forest floor. The values of all other independent variables were constant and equal to their average values among all watersheds. We found that this physical mechanism affects SoS and is in good agreement with statistical estimates (Figure 3).

4. Discussion

4.1. Mechanisms of Forest Floor Thickness Effects on Phenology

Our study is the first to link forest floor thickness (*h*) to plant phenology. A deciduous forest floor is composed of a layer where the release of nutrients from decomposing organic matter is the greatest and has the highest fine-root activity (Schultz, 1972). Although the summer maxima of root and shoot production in temperate forests can vary significantly (Steinaker et al., 2010), the spring flush of fine roots and green-up dates are usually well correlated (Abramoff & Finzi, 2015). In the Adirondack forests of upstate New York the flush of fine roots typically occurs in early April (Burke & Raynal, 1994), which only slightly precedes SoS dates detected for the same type of ecosystems in this study. The initiation of fine-root activity occurs due to spring warming of the forest floor layer above a specific temperature threshold called the "biologic zero" temperature. The biologic zero temperature is the soil temperature that marks the beginning of measurable activity of soil microorganisms (Rabenhorst, 2005). In cold climates this temperature is close to 5°C at a 50 cm depth, which correlates well with the rapid increase of CO_2 efflux in the spring and the flush of fine roots (Barichivich et al., 2012; Pregitzer et al., 2000). Therefore, it is not surprising that our results identify the delay of propagation of temperature through the forest floor as an important and robust mechanism of SoS control.

The agreement between the physical and statistical model, however, is better for the case of 100% soil moisture (Figure 3). This can be explained by the fact that soil moisture in the Adirondack region is

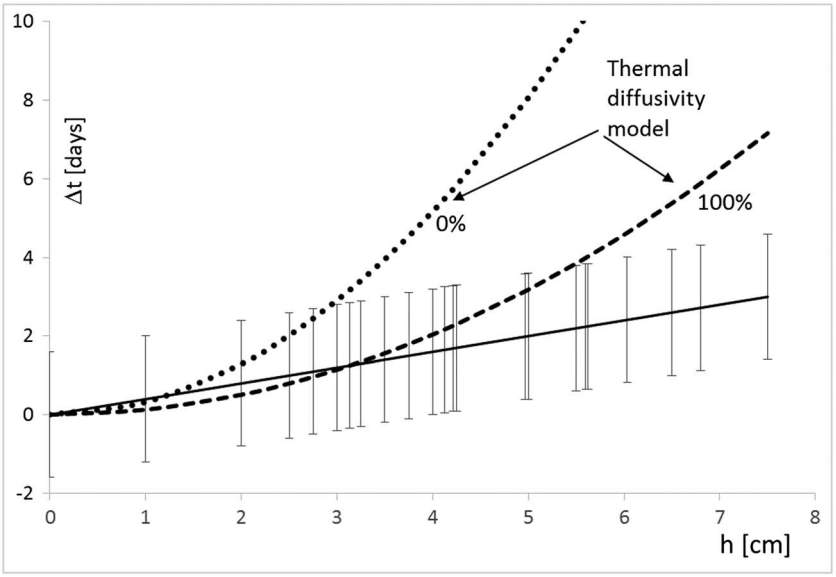


Figure 3. Estimated delay (vertical axis) of spring heat wave propagation (equation (1)) through the forest floor of variable thickness (*h*). These calculations were done for two cases of forest floor moisture: Field capacity (100%) and wilting point (0%). This thermal diffusion model is compared with a two-component, 12-variable PLSR model (solid line) (Tables 1 and 2). Error bars represent the 95% confidence interval. The standard error was calculated as the average of 26 residuals of the fit of PLSR to the data set.

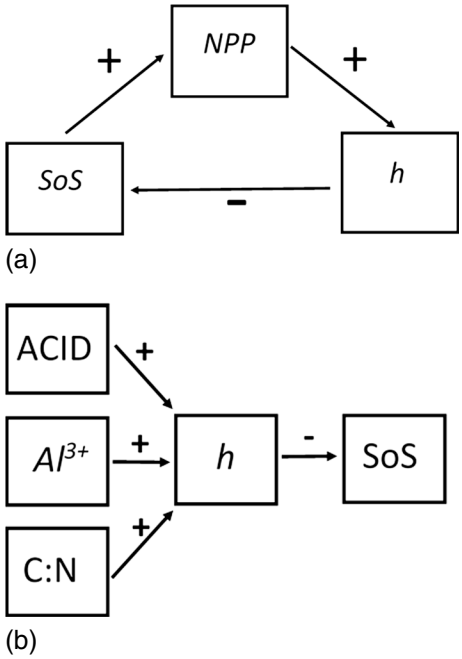


Figure 4. Hypothetical negative feedback between (a) SoS (start of season) and *h* (forest floor thickness), and (b) actual mechanism of forest floor control found in this work. Positive sign above arrows represents positive effect on variable. Early SoS, for example Figure 4a, should lead to higher NPP, and increase in acidity or in C:N ratio (Figure 4b) causes increase in the thickness of the forest floor. Increase in the thickness of forest floor, in turn, causes delay in SoS (negative signs). Abbreviations are as follows: NPP (net primary productivity), ACID (soil acidity status), Al (exchangeable Al), and C:N (soil carbon:nitrogen ratio).

typically high from March to April due to the melting of snow accumulated during winter months (Piatek et al., 2005). When saturated, the forest floor of deciduous stands can hold about twice as much water as its dry weight (Schroeder & Buck, 1970). The fraction of water in the soil Oa horizon has a strong impact on thermal diffusivity of this layer (λ) (equation (2)). According to our estimates, the resulting λ was in the range of $0.6 \pm 0.3 \times 10^{-7}$ ($m^2\ s^{-1}$; Table 3). Note that the derived λ values are about 5 times smaller than the typical thermal diffusivity of seasonal snow (Oldroyd et al., 2013). Therefore, the insulating capacity of the 5 cm of forest floor at 50–100% saturation is equivalent to that of approximately 20–30 cm of snow. Depending on the level of soil moisture, a 5 cm thick layer of forest floor should delay SoS by about 3 to 8 days (Figure 3).

There is one possible conceptual problem in our explanation of this mechanism. If a thicker forest floor leads to a later SoS, it could also result in an overall shorter growing season, lower NPP, and, consequently, thinning of the forest floor, but only if decomposition rates are not affected. According to the same mechanism, a thinner forest floor should cause earlier SoS dates, which would eventually lead to a higher NPP and a thickening of the forest floor. This chain of events could form a negative SoS → NPP → forest floor → SoS feedback mechanism resulting in a decrease of spatial variability for forest floor properties and SoS dates (Figure 4a). To test this possible negative feedback between the forest floor and SoS, we need to consider the factors that control forest floor thickness (Table 4).

The thickness of a forest floor is largely regulated by two competing processes: (1) the decomposition of organic matter within the forest floor, and (2) carbon inputs from litterfall and belowground root turnover. The input of organic carbon into a forest floor is a function of NPP, whereas the decomposition rate of soil organic matter

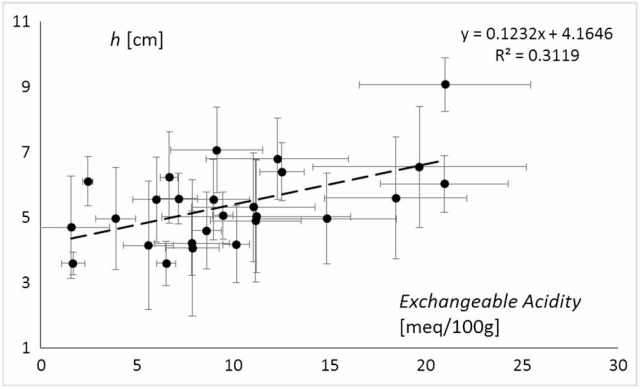
Table 4
Estimates of an Indirect Effect of SoS on Edaphic Variables in the PLSR Model

Y	Regression coefficient r_0 $Y = r_0 \times X \pm \sigma$	Multiple regression coefficient r_1 $Y = r_1 \times X + r_2 \times M \pm \sigma$	Indirect effect ($r_0 - r_1$)	Standard error
K^+	**−0.029**	**−0.021**	−0.008	±0.010
H^+	**−0.181**	**−0.246**	0.065	±0.126
h	**0.114**	0.088	0.026	±0.056

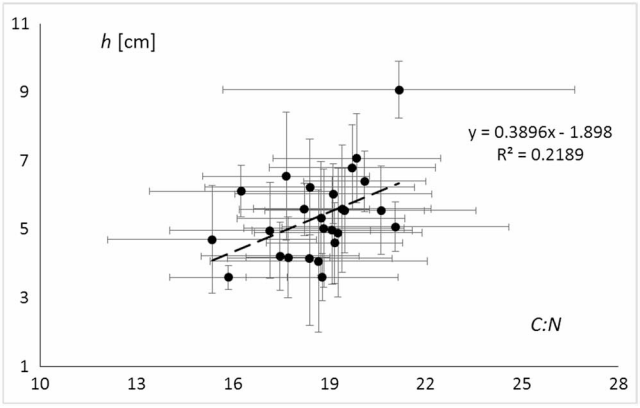
Note. Marked (in bold) regression coefficients r_0 and r_1 are significant at $p < 0.05$. Variable X represents SoS and M represents total exchangeable acidity. Significance of an indirect effect was estimated through the method of bootstrapping ($N = 100$) of standard errors (Shrout & Bolger, 2002). All indirect effects of SoS on edaphic variables are not significant as shown by comparing standard errors with values of an indirect effect. Abbreviations are as follows: K^+ (exchangeable K+), H^+ (exchangeable H^+), and h (forest floor thickness).

(SOM) depends on many environmental variables, including temperature, soil moisture, and SOM chemistry (Lambers et al., 2008). Nonetheless, we found no simple correlation between NPP and h (no zero-order relations) ($R^2 = 10^{-5}$, $p > 0.7$). Instead, forest floor thickness demonstrated significant positive correlations with three other variables: exchangeable acidity (EXA), C:N ratio, and total radiation (Table S7). The first two (Figures 5a and 5b) had the highest probabilities and R^2, and they both represent possible controls on SOM decomposition rate.

Typically, temperature is the most important control of SOM decomposition rate. In our study, however, the entire range of changes in the mean annual temperature across all 26 watersheds is less than 2°C (Table S3). Considering first-order kinetics and the increase in decomposition of SOM by a factor of 2 for every 10°C change in temperature (Arrhenius constant) (e.g., Davidson et al., 2012), we estimate that changes in the decomposition rate due to temperature variability across the 26 watersheds should not exceed 20% (D'Orangeville et al., 2013). The actual range of variability in the thickness of forest floor is much larger and exceeds 250% (Table S3). Similarly, total radiation, which correlates well with temperature, cannot be a significant regulator of SOM decomposition. In our study, this variable changed by only 18% (Table S3).



(a)



(b)

Figure 5. Regression between thickness of forest floor (h) and factors controlling decomposition of SOM: (a) exchangeable acidity ($R^2 = 0.31$, $p < 0.05$), (b) C:N ratio ($R^2 = 0.22$, $p < 0.05$). Vertical and horizontal bars represent errors. Error analysis and calculations of error propagations are shown in Table S4.

Under the above conditions, variability in the chemical composition of SOM could be a conspicuous factor compared to less variable temperature or radiation. Al-organic binding, for example, tends to stabilize organic matter in acidic forest soils (Kunito et al., 2016; Scheel et al., 2007). The decreased mobility of organic carbon has been experimentally linked to the direct effect of increased soil acidity (Evans et al., 2012). The range of Al^{3+} variations among watersheds is 760%. Therefore, it is possible that this factor could significantly contribute to spatial variability in SOM decomposition rate and to forest floor thickness.

Another factor related to forest floor thickness is the C:N ratio, which varies across the 26 study watersheds from approximately 15 to 21 (Figure 5b and Table S3). Decomposers typically have C:N ratios much lower than that of SOM (e.g., Swift et al., 1979), which can lead to faster decomposition of N-rich organic residue (Manzoni et al., 2008). As such, under conditions of small spatial variability in NPP (18%), higher C:N ratios and higher concentrations of exchangeable Al^{3+} could both contribute to the accumulation of organic matter and the thickening of the forest floor. In the case of Adirondack watersheds, where spatial variability in the thickness of a forest floor is controlled mostly by the chemical composition of SOM, it seems reasonable to dismiss the hypothesis of negative feedback (Figure 4a) between forest floor thickness and phenology. The most plausible sequence of events in this mechanism of the effects of h on SoS is as follows. The concentration of exchangeable Al^{3+} and C:N ratio

controls the spatial variability of forest floor thickness *h*, which in turn controls the rate of soil warming and the timing of trees becoming active after winter dormancy (Figure 4b).

4.2. Possible Mechanism of Potassium Effect on Phenology

The mechanism of exchangeable K^+ effects on SoS may be related to the role of exchangeable K^+ as a regulator of nonstructural carbon (NSC) transport from phloem to vascular gaps (e.g., Lemoine et al., 2013). A deficit of exchangeable K^+ can lead to immobilization and accumulation of NSC in leaves and the suppression of photosynthesis (Quentin et al., 2015). Earlier in the season, however, when production of new photosynthates is limited, trees use NSC stored from the previous season as a source of building material for new leaves and other tree parts (Quentin et al., 2015). Therefore, at low exchangeable K^+ levels, the translocation of NSC from their storage locations to new organs might be inhibited. Moreover, exchangeable K^+ in plants can trigger the formation of starch synthesizing an enzyme (starch synthetase) (Murata & Akazawa, 1969). Thus, in addition to enhancing the process of NSC translocation, exchangeable K^+ also stimulates the formation of starch, a very important form of NSC storage. The ability of trees to use this NSC storage early in spring could be an important factor for the successful formation of new buds and leaves.

4.3. Possible Effects of Exchangeable H^+ and ACID Variables on Phenology

In previous work, soil pH was identified as a regulator of the spring phenology of trees (Arend et al., 2015; Wielgolaski, 2001); however, the methods utilized for soil pH measurements were not specified in those studies. Here we found no linkages between SoS and pH, whether it was measured in deionized water or in 0.01 M $CaCl_2$. Although pH, exchangeable H^+, and ACID are all related to soil acidity, these variables reflect different soil properties and processes. Soil pH, as we measured it, was largely a function of soil water chemistry and hydrogen ion weakly adsorbed to soil surfaces, whereas exchangeable H^+ was determined by an extractant that was nearly 100 times more concentrated than the extractant used in measuring pH. The mobility of aluminum in soil increases with increasing acidity, but concentration of inorganic monomeric aluminum, the form mobilized by acidic deposition, is not a function of acidity when soil base saturation is greater than 17 (the aluminum mobilization threshold), which was the condition for approximately one third of the study watersheds (Lawrence, McDonnell et al., 2017). Furthermore, aluminum mobility is also controlled by complexation with soluble organic matter, which generally renders the aluminum nonharmful to plants, but can also influence concentrations of exchangeable Al^{3+} (Dijkstra & Fitzhugh, 2003). As a result, concentrations and forms of soil aluminum can vary widely in soils with similar pH or base saturation values (Cronan & Grigal, 1995).

The factors discussed above can explain why our results do not necessarily relate to previous studies linking pH to SoS. Nevertheless, there are physiological reasons why the ACID(A) variable might delay SoS. In acidified soils, available aluminum binds to fine-root tips limiting the uptake of calcium and magnesium (Shortle & Smith, 1988). Elevated levels of exchangeable Al^{3+} were linked to decreasing ratios of net photosynthesis:dark respiration (McLaughlin & Tjoelker, 1992), increased concentrations of biochemical stress indicators in foliage (Minocha et al., 1997), and increased rates of root turnover and accumulation of fine-root necromass (Godbold et al., 2003). Furthermore, trees growing on highly acidified soil have shown decreased sensitivity to variations in temperature (Lawrence et al., 2005) as they have to allocate more resources toward a stressed root system (Lapenis et al., 2013). These results are entirely consistent with our findings and explain why the earlier start of root growth and SoS is problematic in watersheds where acidic deposition has mobilized soil aluminum.

5. Conclusions and Implications

The forest floor serves an important role as an interface between living vegetation and soil and has several well-known ecosystem functions, including serving as habitat for decomposers such as protozoa and insects, providing plants with storage for nutrients and moisture, serving as a shelter for soil borrowing organisms, providing fuel for forest fires, etc. Our work points to an additional new role of the forest floor as a modulator of the climatic drivers controlling the rate of spring soil warming and the recovery of trees from winter dormancy. This conclusion is supported by a robust statistical analysis as well as by a process-based model. In addition to uncovering the role of forest floor thickness as a constraint on watershed phenology, we

conclude that concentrations of exchangeable H^+, exchangeable K^+, and the mobilization of aluminum by acidic deposition that occurs in the watershed are important chemical controls of SoS timing.

Our findings provide new insights regarding the effects of chemical recovery from past soil acidification and increases in climate warming on forest phenology and productivity. Lawrence et al. (2015) recently found a decrease in acidity, and in particular of exchangeable Al^{3+} concentrations, in the forest floor over a large region of eastern North America over the last 30 years due to decreases in atmospheric acidic deposition. As follows from this work, a decrease in soil acidity could lead to early SoS dates through a biochemical effect on plant physiology. Additionally, soil recovery from acidic deposition could also play a role in forest floor thinning through promotion of higher decomposition rates from decreased organic aluminum binding as exchangeable Al^{3+} concentrations decrease. Forest floor thickness could decline due to warmer temperatures that increase the decomposition rates of SOM. Alternatively, the recent increase in NPP of northern forests (Li et al., 2016) could, under the assumption of unchanged decomposition rates, increase the accumulation of SOM and thereby increase the thickness of forest floors and delay advances in SoS dates, but we do not see clearer evidence of that effect in the study region to date. The resulting contribution of these changes to future trends in forest phenology is difficult to assess. Further work is needed to better understand the physical and biochemical mechanisms linking climatic, landscape, and edaphic factors to the complex system of interacting phenology modulators and drivers.

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