July 2nd, 2015

Editor for *Biogeosciences*

Dear Editor Dr. Williams,

Thank you for the support of this study. We are re-submitting the manuscript entitled "Probing the past 30-year phenology trend of U.S. deciduous forests" to *Biogeosciences*.

All three reviewers suggest more discussion of model uncertainties and analyses of the impacts of species aggregation on the predicted phenological trend. As a result, we added a new paragraph in section 4.2 to discuss uncertainties from the model structure, climate variability, and data availability (or incompleteness). We performed two additional sensitivity tests (simulations 4 and 5), each of which uses parameters calibrated based on species with either the lowest or the highest temperature sensitivity, to quantify modeling uncertainties from the intraspecific variations (see section 4.3 and new Figure S18). We included a recent remote sensing study by Buitenwerf et al. (2015) in the comparison of modeling trends with the ensemble of observations (revised Figure 7). We explained more clearly how we derive observed phenological dates from different products (see supplement and many changes embedded in the main text) and how to calibrate model (see new Tables S4 and S5). We appreciate comments from all three reviewers that have improved this study.

Please find our point-to-point responses below to your decision letter as well as the comments from three reviewers. The line numbers listed in this response are correspondent to the revised manuscript without tracking changes, which has been submitted separately. A mark-up version of manuscript is attached with this response at the end. The original comments are shown in black with our responses marked as blue.

Thanks for your consideration of our submission.

Sincerely,

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Responses to Editor Dr. Williams

Dear Authors:

I have now read the reviews of your submission and examined the evaluations of the authors. Overall the reviews are supportive, and your manuscript should be acceptable for publication after some revisions, which I will review.

In adjusting your manuscript, please respond to each point of the reviewers, and clearly annotate the changes.

Particularly address the following critical points:

Clearly address the issue of species-level responses, evaluating the generality of your model at species level, and the implications of community diversity on phenology. If the PFT concept is being challenged, what does this mean for your model, and its generality?

- → In response to reviewers' comments, we have estimated the impacts of species-aggregation on the estimated forest phenology in sections 4.2 and 4.3 in the following steps:
- (1) We discussed the possible uncertainties of PFT-level simulation in response to the comments from reviewers 1 and 3 as follows (section 4.2, Lines 616-625):

"Third, we choose to calibrate the phenological parameterization at the level of plant functional type (PFT) because species-specific measurements are usually incomplete in time and uneven in space. Such incompleteness may influence the accuracy of derived decadal phenological records used for both model calibration and validation. At the same time, PFT-level parameterization may be too broad for the vegetation modeling because it fails to capture intraspecific variations (Van Bodegom et al., 2012; Reichstein et al., 2014). Observations at the community level suggest that the budburst of some species is sensitive to fall/winter and spring warming but with opposite signs (Cook et al., 2012). In the next subsection, we examine the records of 13 deciduous tree species at Harvard Forest".

(2) We explained why we use PFT-level parameterization in this study (section 4.3, Lines 633-639):

"We do not perform the species-specific simulation for the following three reasons. First, the species-level measurements are usually not available on the continental scale, which influences both model calibration and validation. Second, species-level modeling increases the complexity and computational costs while decreasing predictive reliability (Prentice et al., 2015). Third, investigations at both site level and continental scale show similar temperature sensitivity of tree phenology between the species-specific and species-aggregation approaches."

- (3) We show that temperature responses of plant phenology are similar for individual species at Harvard forest (Figure 8 and corresponding discussion in section 4.3, Lines 641-669, not shown here because they are not revisions)
- (4) We analyzed continental-scale phenology using derived parameters calibrated with different species, in response to comments from reviewer 2 (section 4.3, Lines 671-683):

"We perform two sensitivity runs to evaluate the modeling uncertainties due to intraspecific variations at the continental scale (Fig. S18). Simulations with either the lowest (simulation 4) or the highest (simulation 5) temperature sensitivity yield very similar phenological trends as that in the control simulation (simulation 2). In the East, simulation 4 predicts a spring advance by 0.33 day yr⁻¹ while simulation 5 predicts an advance by 0.35 day yr⁻¹, both of which are close to the 0.34 day yr⁻¹ from the control run. In the West and Northeast, both sensitivity runs predict autumn delay by 0.13-0.15 day yr⁻¹, lower than value of 0.14-0.16 day yr⁻¹ from control run, suggesting that site-level responses may not be necessarily consistent with responses at the continental scale. Both the similar temperature sensitivity at site level (Fig. 8) and the predicted phenological trends at continental scale (Fig. S18) support the concept of phenological modeling at the forest and PFT level, and corroborates the further investigation of phenology-climate interactions at the continental and global scale."

The model validation is not totally clear – I am expecting thousands of evaluations against NPN data, but see only a few dozen points in fig 3. Please clarify. The continental-scale validation is critical to explain, and needs to address bias, random error and correlation.

→ We have clarified in the figure caption of Fig.3 as follows:

"The number of sites shown in the plot is much fewer than the total of 588 because only a small portion of the sites has continuous records for both years and a stringent screening process is applied to derive phenological dates (see Supplement)."

In the supplemental material (the main text is already a little bit lengthy), we added following descriptions to explain how we derive the NPN phenological dates at each site:

"We also derive phenological dates for the USA National Phenology Network (USA-NPN). The network has limited records before 2009 but is significantly enriched thereafter. Currently, there are >600000 records for >20000 individual plants at >6500 sites. Due to the large data amount, we select observations during 2011-2012 for 52 deciduous tree species that are the most common in the U.S. (Table S1). In total, we have records at 588 sites (Table 1); however, not all of these sites provide continuous year-round observations. We apply the following stringent screening filter to derive the phenological dates with high confidence. Each USA-NPN record reports 2-10 phenological statuses, including breaking leaf buds, >=75% of full leaf size, >=50% of

leaves colored, >=50% of leaves fallen, all leaves fallen, and so on. We determine budburst date as the first day with 'breaking leaf buds' and dormancy onset as the first day with 'all leaves fallen'. To ensure that the selected date is the real 'first day' for the phenological shift, we require that there is at least one record beforehand showing no onset of the phenological events. For example, a record with true status of 'breaking leaf buds' is not used if no records in the earlier days of this year report a false status for the same event. The derived dates for individual trees are averaged among species for every site to achieve the spatial distribution of phenology."

We have added following analyses for the continental-scale validation as suggested.

"The simulated spatial pattern is consistent with phenology records from the USA-NPN network, with a correlation coefficient of 0.77 over 46 sites (Fig. 3b). However, the predicted budburst date at these sites is 5 days on average later than the observations. Causes of such bias are unclear but might be related to the uneven spatial distribution of network sites, the distinct nature of the protocols between calibration and validation data, and the incompatibility between model parameters derived at regional scale versus those for the continental scale." (Lines 445-451)

"The validation against observations from 23 USA-NPN sites yields a significant correlation coefficient of 0.80 for the simulated autumn phenology (Fig. 3d). Similar to the spring budburst, predicted dormancy onset is later by 11 days than the observations." (Lines 454-457)

In response to your next comment, we also added more analyses and discussion of the temporal variations of simulated phenology at continental scale (see the responses below).

I agree with the reviewer that "p < 0.2 is a very generous threshold". I do not follow your response. Please think carefully about this issue.

 \rightarrow We have recalculated the correlations with a more stringent threshold of p<0.1 in this revision. We also explained the implications of these new results as follows (Lines 463-472):

"The correlations between modeled and observed budburst dates are larger than 0.3 for 47 out of 59 sites, among which 26 are significant (p<0.1), suggesting that the predicted interannual variation and long-term trend of spring phenology are generally reasonable on the continental scale. The insignificant correlations at 33 sites are in part attributed to the deviations in species between model (PFT level) and measurements (species level). Furthermore, the record length may also contribute to these biases because 28 out of the 33 sites with insignificant correlations have records shorter than 8 years. The large interannual variability in the spring phenology (see section 4.1) may affect the correlations especially for time series with short record length."

I looked at the Buitenwerf paper and it seems to me there are comparisons that you could usefully make with their figure 2 and 3. Figure 2c might be at odds with your results, and would be worth discussing.

→ We compared our results with that in Buitenwerf et al. (2015) as suggested. However, we based our comparison on Figures S2 and S3, instead of Figures 2 and 3. The figures in the main text show standard deviations, which are not the absolute changes in phenological dates but a measure of the severity of change. The figures in the supplement show changes in the seasonal cycle of NDVI for the 1980s and 2010s, which can be used as an indication of phenological changes. In the main text, we compared our results with that in Buitenwerf et al. (2015) as follows: (section 3.3, Lines 521-530)

"In a recent study, Buitenwerf et al. (2015) found an overall extension of the growing season over boreal and temperate forests during 1981-2012 based on the Normalized Difference Vegetation Index (NDVI) from satellite data. However, the exact phenological changes that underlie such overall greening differ among regions. For U.S. forests, the longer growing season is primarily driven by later leaf-off dates, though regional advance of spring is also observed. Our results are generally consistent with their conclusions but with some deviations. For example, they observed later autumn in almost all the eastern U.S., where we predict delays only in the North and Northeast (Fig. 5b). Such discrepancies reflect prediction biases, and may also be a consequence of satellite retrieval uncertainties (Table 1)."

We also added the results of Buitenwerf et al. (2015) in Table 1 and Figure 7 to extend our comparisons with ensemble estimates from multiple literature using remote sensing data. The updated Figure 7 shows distributions of phenological changes even closer to our prediction (Figure 5) than the original results, further supporting our estimate of the phenological trends in U.S. using the well-calibrated model.

Please also examine the structure of the text to improve the focus of the Results section and provide a longer and separate Discussion section. This helps the readers

- → We have moved all the original section 3.4, which discusses the uncertainties of the simulation, to an independent section 4 as Discussion section. Relative to the original version, we have added the following paragraphs to further discuss model uncertainties:
- (1) Uncertainties due to model structure (i.e. whether the model should include chilling and photoperiod limits) (Section 4.2, Lines 602-625)

"Our investigation of the roles of chilling and photoperiod is sensitive to the model structure, climate variability, and data availability. First, the similar performance between spring warming and chilling models might also result from the inaccurate representation of chilling / photoperiod mechanisms. For example, the chilling units used in our parameterization is calculated based on daily average temperature, while Piao et al.

(2015) suggested that leaf unfolding dates during 1982-2011 are triggered by daytime more than by nighttime temperature. The up-to-date autumn phenology model fails to capture interannual variability of dormancy onset (Fig. 2), suggesting that unknown processes are involved in the autumn leaf fall (Keenan and Richardson, 2015). It is unclear whether these processes are related to the variations of photoperiod. Second, the decadal changes in temperature may mask the role of chilling. The trend of winter warming is not significant for most areas in the U.S. (Fig. S14a), suggesting that chilling requirements have been fulfilled in the past 3 decades. However, it is unclear whether the winter warming will intensify in the future, which may slow the advancement of spring budburst. Third, we choose to calibrate the phenological parameterization at the level of plant functional type (PFT) because species-specific measurements are usually incomplete in time and uneven in space. Such incompleteness may influence the accuracy of derived decadal phenological records used for both model calibration and validation. At the same time, PFT-level parameterization may be too broad for the vegetation modeling because it fails to capture intraspecific variations (Van Bodegom et al., 2012; Reichstein et al., 2014). Observations at the community level suggest that the budburst of some species is sensitive to fall/winter and spring warming but with opposite signs (Cook et al., 2012). In the next subsection, we examine the records of 13 deciduous tree species at Harvard Forest."

(2) Uncertainties due to species aggregation (Section 4.3, Lines 671-683)

"We perform two sensitivity runs to evaluate the modeling uncertainties due to intraspecific variations on the continental scale (Fig. S18). Simulations with either the lowest (simulation 4) or the highest (simulation 5) temperature sensitivity yield very similar phenological trends as that in the control simulation (simulation 2). In the East, simulation 4 predicts a spring advance by 0.33 day yr⁻¹ while simulation 5 predicts an advance by 0.35 day yr⁻¹, both of which are close to the 0.34 day yr⁻¹ from the control run. In the West and Northeast, both sensitivity runs predict autumn delay by 0.13-0.15 day yr⁻¹, lower than value of 0.14-0.16 day yr⁻¹ from control run, suggesting that site-level responses may not be necessarily consistent with responses at the continental scale. Both the similar temperature sensitivity at site level (Fig. 8) and the predicted phenological trends at continental scale (Fig. S18) support the concept of phenological modeling at the forest and PFT level, and corroborates the further investigation of phenology-climate interactions at the continental and global scale."

best wishes

Mathew Williams

Responses to Reviewers

Anonymous Referee #1

We thank the referee for the positive, helpful and comprehensive review that has improved the manuscript. Detailed point-by-point responses to the reviewer comments are provided below. The reviewers' comments are shown in black with our responses are marked as blue. The line numbers below refer to the revised manuscript to be submitted separately.

General comments

In this contribution, the authors parameterize an ensemble of models of spring and autumn phenophases and use the models (1) to derive continental maps of phenological trends in US deciduous forests over the period of, at most, 1982 to 2012 and (2) to evaluate the role of model components (chilling function, role of photoperiod, GDD/CDD summation) on the predicted trends.

The paper is overall well written though a bit lengthy. I do appreciate the details the authors give on methodological aspects, and the multiple checks (against ground observation and remote sensing data) they present to corroborate their results, but probably some of this material would better be placed in the supplementary material section (see my specific comments). As a formal comment, notice that the "Results" section is more a mixture of results and discussion, while the "Conclusion and discussion" section is rather a "conclusion". I suggest the authors to rename the sections accordingly.

The science is sound, Results are well presented and, considering the spatial extent covered in the paper, new for the US zone (similar results centred on the European zone have already been published, see notably Menzel et al., 2006; Menzel, 2013).

→ We thank the reviewer for positive evaluations. We have moved several parts to the supplementary material as suggested. We changed "Conclusions and discussion" to "Conclusions" and added a separate "Discussion" section.

Some aspects of the paper deserve further discussion / modifications:

(1) Phenological models are usually parameterized at the species level (parameters are believed to be species-specific, referring to species proper characters). The authors choose to parameterize the models on phenological metrics derived from LAI time series acquired in mixed deciduous forests. The model validation is undertaken against an ensemble of data, including a spectrum of forest and non-forest (e.g. Lilac) woody species, which (partly) differ from the species for which the models were calibrated.

Questions related to that aspect:

- The model validation is possibly affected by the choice of averaging at a given site all available phenological data (L2-3 p 6044). The local species composition will obviously affect the observed mean. Furthermore, interrupted pheno time series are frequent, so that i suppose the number of species observed at a given location can change over time, and bias the calculation of pheno average dates.
- The main results of the paper (trends derived from the simulations and the relative little influence of the chilling function / photoperiod on determining the date of budburst / senescence) are dependent on the authors choice (fitting ensemble models over all available data, with no attention to the particular response of a species). Yet, there is evidence in the literature that different, co-existing, species exhibit different phenological trends (in response to temperature changes: see e.g. Vitasse et al., 2009; Fu et al., 2014a). I expect the authors to at least discuss that aspect, and at best to test the genericity of their results with respect to particular species, known to be early/late flushers/senescent.
- The question of model parameterization at the PFT level ("temperate deciduous broadleaf species", DBF) should be linked with recent attempts to re-define PFTs. The validity of the PFT concept for vegetation modelling is under discussion (see e.g. Reichstein et al., 2013; van Bogedom et al., 2012). If all DBF species show similar trends (see my point above), then using a PFT-parameterized model is OK when projecting the future / past of forest phenology
- \rightarrow We agree that data incompleteness and species-aggregation may affect our conclusions. Other reviewers have also raised similar concerns. We considered all the related comments and added the following discussion in the revised paper: (Section 4.2, 602-625)

"Our investigation of the roles of chilling and photoperiod is sensitive to the model structure, climate variability, and data availability. First, the similar performance between spring warming and chilling models might also result from the inaccurate representation of chilling / photoperiod mechanisms. For example, the chilling units used in our parameterization are calculated based on daily average temperatures, while Piao et al. (2015) suggested that leaf unfolding dates during 1982-2011 are triggered by daytime more than by nighttime temperature. The up-to-date autumn phenology model fails to capture interannual variability of dormancy onset (Fig. 2), suggesting that unknown processes are involved in the autumn leaf fall (Keenan and Richardson, 2015). It is unclear whether these processes are related to the variations of photoperiod. Second, the decadal changes in temperature may mask the role of chilling. The trend of winter warming is not significant for most areas in the U.S. (Fig. S14a), suggesting that chilling requirements have been fulfilled in the past 3 decades. However, it is unclear whether the winter warming will intensify in the future, which may slow the advancement of spring budburst. Third, we choose to calibrate the phenological parameterization at the level of plant functional type (PFT) because species-specific measurements are usually incomplete in time and uneven in space. Such incompleteness may influence the accuracy of derived decadal phenological records used for both model calibration and validation.

At the same time, PFT-level parameterization may be too broad for the vegetation modeling because it fails to capture intraspecific variations (Van Bodegom et al., 2012; Reichstein et al., 2014). Observations at the community level suggest that the budburst of some species is sensitive to fall/winter and spring warming but with opposite signs (Cook et al., 2012). In the next subsection, we examine the records of 13 deciduous tree species at Harvard Forest."

- (2) Protocol of model validation: ground observation data from phenological networks are by far the most abundant source of data for validation (see Table 4). The reader would like to see a figure comparing dates derived from LAI metrics to autumn dates derived from phenological observations (Fig. 2 does not report such a comparison for autumn).
- → We have shown more date comparisons between phenological records and LAI-derived ones in the updated Fig. S2. The LAI-derived dates at Harvard Forest are not complete and we mentioned in the SI that: "However, for US-Ha1, date records are comprehensive while LAI measurements are incomplete and as a result we do not use the LAI-derived dates in the model validations at this site (e.g. Fig. 1)". In the main text section 3.4.3, we also explained that: "The 21-year average of the ensemble dormancy onset date is DOY 306, again close to the estimate of DOY 310 based on LAI (Table 3)." These statements and results show that LAI-derived dates are a reasonable proxy for missing phenological records for the model validation.
- (3) The use of the "dormancy" term is not adequate to qualify leaf fall (as derived from LAI measurements or Phenocams). Please remind that dormancy is a physiological state of the bud, starting right after budset (i.e. concomitantly to the timing of height growth cessation, i.e. in the middle of summer, when leaves are still present and green) and ending at budburst during next spring (e.g. Delpierre et al., 2015). Hence, please replace occurrences of "dormancy" by "leaf fall" throughout the manuscript.
- → In the first paragraph of section 2.2, we added the following statement to explain the 'dormancy onset' date: "Most of phenological records are discrete and evaluation of the annual cycle of tree phenology is difficult. Following definitions in earlier literatures (e.g., Zhu et al., 2012), we validate spring budburst dates (or the onset of growing season, the dates D1 in Fig. S1) and dormancy onset dates (or the end of leaf fall period, the dates D2 plus falling length L2 in Fig. S1) predicted by phenology models with the site-level records. The dormancy onset date defined here is based on the canopy level instead of the bud dormancy examined in a recent review paper by Delpierre et al. (2015)." (Lines 172-179)

Specific comments

L25, p 6039: the "temperature sensitivity to altitudinal trends" is not clearly defined. Altitudinal trends are first and foremost T-related. Please rephrase.

→ We have removed this sentence because we do not examine the impacts of altitude on

phenological responses in this study.

- L6-14 p 6041: models calibrated at the species scale cannot pretend to estimate phenological trends for "US deciduous forests", merely for certain species
- → The models were calibrated with derived phenological dates from LAI measurements, which represent the average phenophase of multiple species. We also validated the selected models with average dates across species, though uncertainties exist due to data incompleteness. "Both the similar temperature sensitivity at site level (Fig. 8) and the predicted phenological trends at continental scale (Fig. S18) support the concept of phenological modeling at the forest and PFT level, and corroborates the further investigation of phenology-climate interactions at the continental and global scale." (Lines 680-683)
- L22 p 6041: were data from 1000 ground observation sites used? Not comparable with the 4 ground observation sites used for calibration.
- → We clarify that "In total, phenological observations from 1151 sites were used for model validation." (Line 134)
- L23 p 6042 and on: unclear to me where are the four calibration sites located in the US. Refer to Figure 1 here.
- → In the revised paper, we refer to Fig. 1 even earlier at the first sentence of section 2.1 as follows: "Decadal measurements ... to calibrate parameters of the phenology model (Table 2 and Fig. 1)" (Lines 141-143). We also refer to Fig. 1 in one sentence before the original L23 P6042. (Now Line 166).
- P 6042 §2: only four out of the 5 calib sites are mentioned (Hubbard Brook missing). Is it because the LAI data were not available at the US-HB site? In that case, against which data were the model calibrated for US-HB?
- → No, the LAI data were not available at the US-HB site. We do not use data from US-HB site to calibrate model parameters. Instead, we use the phenological dates at this site to validate the calibrated models and to check whether these models could perform well at locations beyond the calibration sites.
- P 6045: equations 6 and 7: which arguments have driven the choice of the parameters to optimize / to fix?
- → The fixed parameters in Equation 6 and 7 were adopted from Chuine et al. (1999). We calibrated other parameters based on RMSE between model prediction and observations. We presented all the calibrated parameters in Table S4.

Equations 2 to 12: report parameters units in the text, or in a dedicated Table.

→ Both the values and units of the optimized parameters have been shown in the new Table S4.

Equations 8 and 11 share the same variable name (f_T) for two independent variables. Use different names.

 \rightarrow The name of spring phenology has been changed to f_S .

L17-20 p 6049: conditions of the SA are unclear to me. Please reconsider and rephrase.

→ We further explained the sensitivity analysis as follows: "In this run, we do not include chilling constraint for the spring phenology by using a fixed and calibrated forcing threshold F^* of 50 degree days. As a result, forcing value S_f begins accumulation from winter solstice and budburst occurs if only $S_f > F^*$. The whole process is not dependent on the value of chilling units S_c . Meanwhile, we lift the photoperiod cap for leaf senescence by setting $f_P = 1$, so that the autumn phenology is only determined by temperature ($f_A = f_T$)." (Lines 367-372)

L10 p 6050: replace "decreasing" by "increasing" (higher AIC means the model has a worse accuracy-parameterization trade-off).

→ Yes, we have corrected 'decreasing' to 'increasing' as indicated.

L15-16 p 6050: which physiological processes do you point here? What are the "synthesis, viscosity, diffusion" processes you mention? Which role do they / are they supposed to play in leaf senescence? If no precision is given, this sentence should be deleted.

- → Physiological processes are important for plant phenology. For example, "the abundance or concentration of enzymes is determined by the rates of synthesis and breakdown. It is known that temperature and photoperiod play a prominent role in controlling these processes. Temperature, for instance, can act through purely physical mechanisms, as when it influences viscosity and diffusion" (Schaber and Badeck, 2003). However, we understand that physiological impacts are very uncertain and the specific pathway is unclear. We have deleted both this sentence and the one in the discussion section for clarity.
- L 24 p 6051 and on: I'm not a native English speaker, but I've always read calendar date to be reported as DoY XXX rather than XXX DoY
- → We have changed all the 'XXX DOY' to 'DOY XXX'.

L15-17 P 6053: compare with altitudinal trends in Vitasse et al. 2009

 \rightarrow We have added the following statement: "The temperature sensitivity of spring budburst date is also within the range from -2.05 to -7.48 days °C⁻¹ for different species

based on the field experiments performed by Vitasse et al. (2009)." (Lines 505-507)

L9 p 6056: the question of the species-specificity of phenological model parameters is well established (see Vitasse et al., 2011 for instance). I would write "has been shown" instead of "is thought".

→ We have changed "are thought" to "have been shown" as suggested.

L10 p 6056: a key missing reference reporting results for one of the datasets used in the paper is Archetti et al. (2013)

→ Yes. We have cited Archetti et al. (2013) in the revised manuscript.

L26 P 6058: The sentence beginning with "Missing. . ." should be rewritten, with appropriate places for parentheses and citations. Again, the notion of "synthesis" cited along the Schaber & Badeck (2003) paper, should be precised or deleted.

→ We have corrected the format errors and removed citation of Schaber and Badeck (2003) for clarity.

L 1 p 6059: the potential link between spring and autumn phenophases was demonstrated in the Fu et al. (2014b) paper. This citation should appear along with the Keenan & Richardson (2015) paper.

→ We have cited Fu et al. (2014) PNAS as suggested.

Section 3.1.2 and Figure 3: predicted dates are systematically biased (occur later than the ground observed dates). Probably caused by the distinct nature of the protocols used for obtaining calibration data vs. validation data. This should be investigated and reported in the paper.

→ We examined this issue in the revised manuscript: "However, the predicted budburst date at these sites is 5 days on average later than the observations. Causes of such bias are unclear but might be related to the uneven spatial distribution of network sites, the distinct nature of the protocols between calibration and validation data, and the incompatibility between model parameters derived at regional scale versus those for the continental scale." (Lines 447-451) For autumn phenology, we added: "Similar to the spring budburst, predicted dormancy onset is later by 11 days than the observations." (Line 456)

Figure 1: 5 sites are mentioned on the map, only 4 sites appear on the graphs. Clarify. Replace "literature-based phenology model" by "models S9 and A4" in the caption

→ We added the following figure caption to clarify: "Derived phenological dates at US-MOz are used for model calibration but not validation and are not shown here." We

corrected the names of phenology model as suggested.

Figure 4: no autumn data appear on the figure, contrary to what is reported in the caption.

→ We have removed the words "and autumn model A4" to make sure that this figure is for validation of spring dates.

Figures 6 should be moved to the Suppl. Mat. Section.

→ The original Figure 6 has been moved to SI (now Fig. S14) as suggested.

Table 1: numeric values of the trends should be reported, and discussed in section 3.3

→ Reviewer #3 also proposed the similar comment. This is a good suggestion but might be difficult to implement for two reasons. First, regional phenological changes varied significantly across the U.S., while most of previous studies, if provided numeric values, show only numbers on the continental scale or for the latitude belts. For example, Jeong et al. (2011) reported almost zero changes in start of season over U.S. for 1982-1999. However, at the regional scale, this study showed both positive and negative trends in U.S. Second, the definition of phenological events varies among different studies (White et al., 2009), making it difficult to quantitatively perform the inter-comparison. As a result, we qualitatively compared phenological changes based on spatial maps from those studies, so as to estimate the ensemble spatial distribution of phenological changes in the past decades.

Table 2-3: Four sites appear, when sites are cited in the text (p 6042) for calibration. Clarify.

→ We clarified as follows: "Data from three out of the four calibration sites (US-Ha1, US-UMB, US-MMS, Table2 and Fig. 1) are also used for validation; however, we use them in different ways."

Table S3: categorize spring and autumn parameters.

→ We categorized parameters for spring and autumn models as suggested.

Figure S8: "CDD-photoperiod model" has changed name to "literature-based" (compared to e.g. Fig. 9)

→ The figure title has been changed to "CDD-photoperiod model" as indicated.

SI, section 1 ("Derivation of phonological observations"): no mention is made to the autumn pheno dates. Are the LAI threshold used identical to those for spring?

→ Yes. We clarify in the SI as follows: "The same spring LAIt is applied to derive dormancy onset dates, which also show low RMSE against other sources of autumn phenology (Fig. S2b)."

Anonymous Referee #2

We thank the referee for the positive, helpful and comprehensive review that has improved the manuscript. Detailed point-by-point responses to the reviewer comments are provided below. The reviewers' comments are shown in black with our responses are marked as blue. The line numbers below refer to the revised manuscript to be submitted separately.

General comments

I have read the discussion paper "Probing the past 30-year phenology trend of U.S. deciduous forests" by Yue et al. with great interest.

In this paper, the authors test a suite of phenology models against site-level data in the US. Models represent spring budburst and autumn dormancy with various degrees of complexity as shown by differences in the required input data and the number of parameters. Models are first calibrated against phenology observations at four deciduous forests. Then, the selected best spring and autumn models are used to produce time series of phenology for the last 30 years over the whole conterminous US. The authors conclude to a temperature-driven advance in the spring budburst in the East and a delay in dormancy in the Northeast and West with large regional variations.

Phenology in ecosystem models is a topical question and this study falls well within the scope of the journal. The paper is well-written and easy to follow but I have several comments about the modelling procedure that needs to be clarified before publication (see below).

My main comment is that most of the spring phenology models have been derived from the same site, and calibrated against only 4 sites. How reliable are these models once applied to represent forests with varying species composition under very different climatic conditions? An assessment of the uncertainty in at least the models used to produce the regional maps is needed to check whether trends are a robust, or a result of over-fitted models.

→ We fully agree that the assessment of modeling uncertainty is important for the understanding of the robustness of our model predictions. In this study, we have quantified impacts of climate variability, model structure, and species aggregation on the predicted phenological trends. We also discussed the uncertainties from other possible sources, such as the incompleteness of observations, unrealistic representation of chilling/photoperiod limits, incompatibility of model parameters at site-level and continental scales, and so on.

We performed two additional sensitivity tests and added a new figure S18 following the reviewer's comment. "We analyze species-specific temperature sensitivity of tree phenology at Harvard Forest (section 4.3). Based on these results, we perform two additional sensitivity tests to evaluate modeling uncertainties from the intraspecific

variations. In the first run (simulation 4), phenological parameters are derived based on records of species with the lowest temperature sensitivity for both spring (Sweet Birch, *Betula Lenta*) and autumn (Paper Birch, *Betula Papyrifera*). In the other run (simulation 5), parameters are derived using records of species with the highest temperature sensitivity for spring (Striped Maple, *Acer Pensylvanicum*) and autumn (Black Oak, *Quercus Velutina*). We applied the derived parameters for the whole domain of U.S. by ignoring the realistic fractional coverage of specific species, so as to estimate the maximum uncertainty of prediction due to the intraspecific variations." (Lines 374-384)

"We perform two sensitivity runs to evaluate the modeling uncertainties due to intraspecific variations on the continental scale (Fig. S18). Simulations with either the lowest (simulation 4) or the highest (simulation 5) temperature sensitivity yield very similar phenological trends as that in the control simulation (simulation 2). In the East, simulation 4 predicts a spring advance by 0.33 day yr⁻¹ while simulation 5 predicts an advance by 0.35 day yr⁻¹, both of which are close to the 0.34 day yr⁻¹ from the control run. In the West and Northeast, both sensitivity runs predict autumn delay by 0.13-0.15 day yr⁻¹, lower than value of 0.14-0.16 day yr⁻¹ from control run, suggesting that site-level responses may not be necessarily consistent with responses at the continental scale. Both the similar temperature sensitivity at site level (Fig. 8) and the predicted phenological trends at continental scale (Fig. S18) support the concept of phenological modeling at the forest and PFT level, and corroborates the further investigation of phenology-climate interactions at the continental and global scale." (Lines 671-683)

Specific comments

P6042 L2: Please define "long-term"? Perhaps the term "decadal" would be more suited to describe the station data.

→ Yes. We have revised "long-term" to "decadal" as suggested.

P6043 L18: Would it be more correct to estimate budburst and dormancy based on significant changes in the LAI time series rather than a threshold?

 \rightarrow It is a good suggestion to estimate phenological dates based on rapid changes in LAI. However, LAI records are not continuous, making it difficult to identify those phase changes. For example, measurements at US-UMB in 1999 started at DOY 121 with LAI of 1.5 m² m⁻², which could be considered as the background value of LAI. However, in 2007, measurements began on DOY 132 with LAI of 1.93 m² m⁻². For the year 2007, budburst date could be calculated only by extrapolating LAI to the day with value of 1.5 m² m⁻².

P6045 L1: See my main comments. Also, why is Jolly et al.'s (2005) phenology model not used for spring?

→ We have responded to your main comments. All spring models used for the inter-

comparison considers chilling requirement while Jolly et al. (2005) does not implement such an effect.

P6046 L11: More detailed are needed to describe the calibration method. I am concerned that calibrating "by hand", as it appears, rather than using an automated tool does not allow to find the "true" optimum. Generally, using different model structures introduces more uncertainty than the equifinality of parameters of a single model. However, a few words about how well-defined the parameters are is required here.

→ In the text, we explained that: "For each model in Table 5, we apply the exhaustive enumeration method to evaluate all combinations of the discrete parameters. We select the optimized parameters that jointly predict the lowest RMSE for the long-term budburst dates at the four calibration sites." (Lines 279-282) We have shown the values of optimized parameters in Tables S3 and S4.

P6051 Section 3.1.2: Can you compare these results with satellite based estimates from Buitenwerf et al. (2015)?

→ Section 3.1.2 evaluates spatial distribution of simulated phenology while Buitenwerf et al. (2015) estimates changes in the standard deviation of phenological metrics. The two studies are investigating different aspects of phenology, making it difficult to perform the comparison directly.

P6052 L12: p < 0.2 is a very generous threshold

→ We have recalculated the correlations with a more stringent threshold of p<0.1 in this revision. We also explained the implications of these new results as follows (Lines 463-472):

"The correlations between modeled and observed budburst dates are larger than 0.3 for 47 out of 59 sites, among which 26 are significant (p<0.1), suggesting that the predicted interannual variation and long-term trend of spring phenology are generally reasonable on the continental scale. The insignificant correlations at 33 sites are in part attributed to the deviations in species between model (PFT level) and measurements (species level). Furthermore, the record length may also contribute to these biases because 28 out of the 33 sites with insignificant correlations have records shorter than 8 years. The large interannual variability in the spring phenology (see section 4.1) may affect the correlations especially for time series with short record length."

Figures Please add coordinates on Figures 3 to 7.

→ Coordinates have been added as suggested.

In Figure 3, why do the coloured surface appear to have different shapes in panels a and c, especially in the Southeast? Is it an artefact due to the colour scale that draws missing

areas and areas with lower values in white? More generally, why are the coloured areas in all maps different from the map in Figure 1?

→ Yes, the inconsistency between a and c is due to lower values in white. A full coverage of DBF has been shown in Figure 1. We have clarified in the caption of Figure 3 as follows: "The coverage of colored patches in (a) and (c) differs from that in Figure 1 because values at and beyond the low end of color scales have been shown in white."

Anonymous Referee #3

We thank the referee for the positive, helpful and comprehensive review that has improved the manuscript. Detailed point-by-point responses to the reviewer comments are provided below. The reviewers' comments are shown in black with our responses are marked as blue. The line numbers below refer to the revised manuscript to be submitted separately.

General comments

Yue et al studied the changes of both spring and autumn phenology using different spring and autumn phenology models and focus on multiple scales, i.e. in situ and continent, and they found spatial difference in phenology trends over the period 1980-2012. Importantly, they concluded the temperature is the dominant driver of spring/autumn phenology, because phenology models including a chilling requirement or photoperiod limitation does not improve the model performance. The results are interesting, while there are some major comments in the model calibration and evaluation, as well as the explanation of the model results.

The phenology models are normally parametrized for specific species, i.e. difference specie holds different parameters, even at different sites for same specie ... the authors calibrated the model using LAI-based dates (species-mixed), and applied these models in the forest sites that probably have different species composition, as well as for the shrub i.e. Lilac. Uncertainty would be raised, therefore, the best model, which was selected for the continent scale prediction (while, actually the US scale), may be not the best, as the parameters might be not accurate. In additions, the models were calibrated using four site dates. How you calibrate these models, i.e. using mixed-dates from all four sites or using the yearly-average-dates across the 4 sites? Need to be clarify. . .

 \rightarrow The uncertainty of model parameters is one of the main sources of uncertainty in phenological modeling. We include the following text to address this in the revised manuscript: "The validation shows that the predicted spatial pattern is reasonable and the long-term average matches observations within sampling uncertainty (Figs. 3-4). However, due to the data scarcity, all the selected sites are located in temperate areas ranging from 38°-46°N, suggesting that the model should be used cautiously at other latitudes and parameters may require re-calibration." (Lines 710-714)

We clarified how to calibrate models as follows: "The measurements of LAI are not evenly distributed from year to year, and data at some years are too sparse to form the full annual cycle. As a result, we derive the decadal average phenological dates by regressing against all available LAI records at one site." (Lines 153-156) "For each model in Table 5, we apply the exhaustive enumeration method to evaluate all combinations of the discrete parameters. We select the optimized parameters that jointly predict the lowest RMSE for the long-term budburst dates at the four calibration sites." (Lines 279-282)

For the most important conclusion, i.e. the temperature is the dominant driver of spring

and autumn phenology, because the chilling and photoperiod models does not improve the model performance. It's is not completely right. (1) First, for spring phenology, the chilling requirement may be fullfilled, so the similar model performance can be expected, as reported by previous studies that compared different phenology models. So you could not evaluate the chilling effect from the model performance only...(2) Second, the similar model performance between one- and two- phase models may also suggest that the chilling / photoperiod mechanisms may not be accurately represented in these models, such as the chilling units that are counted as the chilling days or is a daily temperature function, while the day and night temperature may be play a different role in phenology (see Piao et al 2015 Leaf onset in the northern hemisphere triggered by daytime temperature). (3) Given the models are reliable, and the temperature might be a dominant driver for phenology in current climate, while with climate warming, the chilling and photoperiod may play an important role, might be dormant in the future. At least, these issues should be discussed in the manuscript. . .

→ We appreciate reviewer's thoughtful comments that reveal possible uncertainties in this study. In combination with comments from other reviewers, we added the following discussion in the revised manuscript:

"Our investigation of the roles of chilling and photoperiod is sensitive to the model structure, climate variability, and data availability. First, the similar performance between spring warming and chilling models might also result from the inaccurate representation of chilling / photoperiod mechanisms. For example, the chilling units used in our parameterization are calculated based on daily average temperatures, while Piao et al. (2015) suggested that leaf unfolding dates during 1982-2011 are triggered by daytime more than by nighttime temperature. The up-to-date autumn phenology model fails to capture interannual variability of dormancy onset (Fig. 2), suggesting that unknown processes are involved in the autumn leaf fall (Keenan and Richardson, 2015). It is unclear whether these processes are related to the variations of photoperiod. Second, the decadal changes in temperature may mask the role of chilling. The trend of winter warming is not significant for most areas in the U.S. (Fig. S14a), suggesting that chilling requirements have been fulfilled in the past 3 decades. However, it is unclear whether the winter warming will intensify in the future, which may slow the advancement of spring budburst. Third, we choose to calibrate the phenological parameterization at the level of plant functional type (PFT) because species-specific measurements are usually incomplete in time and uneven in space. Such incompleteness may influence the accuracy of derived decadal phenological records used for both model calibration and validation. At the same time, PFT-level parameterization may be too broad for the vegetation modeling because it fails to capture intraspecific variations (Van Bodegom et al., 2012; Reichstein et al., 2014). Observations at the community level suggest that the budburst of some species is sensitive to fall/winter and spring warming but with opposite signs (Cook et al., 2012). In the next subsection, we examine the records of 13 deciduous tree species at Harvard Forest." (Lines 602-625)

One more comment, the authors compared the trends of phenology between the modeling and the RS results, but you could not identify the robust of the model results using the RS

data, because the two results are not comparable, i.e. the modeling outputs and the RS data may refer to different phenophase. The statement need to be improved.

→ We agree that the definition of phenological events with RS data is very uncertain. We added the following statement in the revised manuscript: "Since the definition of phenological events varies among different studies (White et al., 2009), we qualitatively compare the simulations with the remote sensing retrievals so as to evaluate the ensemble spatial distribution of phenological changes in the past decades." (Lines 538-541)

Specific comments

P6039 L2: Körner, not Korner, please check through the manuscript;

Körner and Basler discussed the importance of photoperiod on the spring phenology in their science paper. Better to rephrase it as 'is sensitive to temperature variation', and cite review papers, such as Cleland et al 2007; Polgar, C.A., Primack, R.B., 2011.

→ We have corrected the author name of the reference to Körner. We have rephrased the sentence and added those review papers as suggested.

P6039 L10, for the phenology changes in Europe, you should also cite Menzel et al 2006 GCB

→ We have added the suggested reference in the revised manuscript.

P6039 L16, please rephrase as 'some species may require cold temperatures', the chilling may not only occur in winter, also in early spring. . .

→ We have removed the word "winter" as suggested.

P6039 L20, for the tree age, you can cite Vitasse et al 2013: Ontogenic changes rather than difference in temperature cause understory trees to leaf out earlier

 \rightarrow Yes, we have cited the paper as suggested.

P6039 L25, what is the 'temperature sensitivity to altitudinal trends'? Please rephrase...

→ We have removed this sentence because we do not discuss it in the paper.

P6041 L4-8, how you calibrate the models, using average date of all species from the four forests? No clear..

→ We rephrased it as: "We first calibrate each model using derived phenological dates based on the decadal ground observations of leaf area index (LAI) at four deciduous forests." (Lines 115-116) In the discussion section 4.3, we showed that LAI-based phenological dates could be a good indicator of species-aggregated phenology.

P6041 L18, define chilling requirements

→ We have defined it in the introduction section: "Some species may also require cold temperatures before budburst (named chilling requirement)"

P6041 L22, ~1000? Why not provide the exact number of sites?

 \rightarrow We changed it to the accurate site number of 1151 in the revised paper.

P6042 L7, because you determined the phenological dates from the LAI, better use 'Start of growing season' or 'onset of growing season', instead of 'budburst';

→ Our comparison showed that the 'onset of growing season' derived from LAI is very close to the 'budburst' from phenological records (Fig. S2). As a result, we continue to use 'budburst' for the LAI-derived spring phenology. In the revised text, we have the following definitions about spring budburst: "spring budburst date (or the onset of growing season, the dates D1 in Fig. S1)."

P6042 L6-10, D1, L1, D2 and L2, you should point these dates out in a Fig S?

→ We have shown D1, L1, D2, and L2 on the revised Fig. S1a.

P6042 L6-10, you determined the phenological dates for each year, and then calculated the average dates for each site, right? After that, you calibrated the model using only four date, i.e. four average dates from four sites? I'm not sure that, maybe need to rephrase to make it clear;

→ In the revised paper, we clarified as follows: "The measurements of LAI are not evenly distributed from year to year, and data at some years are too sparse to form the full annual cycle. As a result, we derive the decadal average phenological dates by regressing against all available LAI records at one site." (Lines 153-156)

P6042 L14-18, this is results, move to the results section. . .

→ It is a good suggestion. However, as you may read, the result section presents model calibration and validation. The sentences you mentioned here are the introductions of sites and data, and as a result might be suitable for the method section.

P6043 L12-13, to evaluate the model, you used the averaged dates over all trees and species at each site. This means that the difference of average phenological dates among sites not only determined by the climatic variables, but also the composition of species. . . So, the questions is that can the parameters determined at four-sites be applied in other sites that have different species composition?

→ As we respond to the general comments, we tried the best to collect the most complete datasets (phenological records, LAI, and photos) to calibrate parameters and validate

model performance at sites and locations outside the calibration sites. "The validation shows that the predicted spatial pattern is reasonable and the long-term average matches observations within sampling uncertainty (Figs. 3-4). However, due to the data scarcity, all the selected sites are located in temperate areas ranging from 38°-46°N, suggesting that the model should be used cautiously at other latitudes and parameters may require recalibration." (Lines 710-714) We also discussed the uncertainties due to the differences in species composition in the section 4.3.

P6043 L21-25, define the budburst and dormancy when it first occurred. . .

→ We defined them in the revised manuscript: "Following definitions in earlier literatures (e.g., Zhu et al., 2012; Richardson et al., 2013), we validate spring budburst date (or the onset of growing season, the dates D1 in Fig. S1) and dormancy onset date (or the end of leaf fall period, the dates D2 plus falling length L2 in Fig. S1) from phenology models with the site-level records." (Lines 173-177)

P6043 L22, how you define the rapid change from gray to light green? Using the maximum change rate? Difficult to understand the 'the middle of the few days when tree colors change rapidaly. . .'. Please rephrase, as well as the definition of Dormancy start

→ We explained it more clearly in the revised text: "Based on the changes of tree color in these photos, we can easily identify the phase changes in phenology. For example, changes from gray to light green in spring could occur within several days. We select the middle of these few days as the budburst date. Similarly, changes from brown to gray in late autumn may happen within one week and the middle day of the week is selected as the dormancy onset date. An example of autumn dormancy at US-UMB is shown in Fig. S3. The dates derived from photos may have comparable precision as the observations from site-level phenological records (e.g., Fig. S2c), because the latter are also reported weekly or half-weekly." (Lines 197-205)

P6043 L23, the dormancy start normally is around the date when the bud set, i.e. much earlier than the leaf coloring. . . .better use other terms, such as offset of growing season?

→ The 'dormancy' here represents the ending period of leaf fall. It is defined based on the canopy level instead of bud level. In the revised paper, we added following statement: "The dormancy onset date defined here is based on the canopy level instead of the bud dormancy examined in a recent review paper by Delpierre et al. (2015)." (Lines 177-179)

P6044 L22-26, similar model performance of 1- and 2- phase models suggest the chilling maybe sufficient over the study period. You can expect the chilling effect as the large scale, but I did not find the correlation between model performance and difference in phenological response among species, please rephrase ...

→ We have changed the phrase "for most species" to "at the site level".

P6044 L28, The parameter values of the Sarvas function were determined from the experimental results on Betula pendula Betula pubescens and Populus tremula in Finland (Sarvas, 1972). Whether the 'northern' parameters can be used in the temperate trees? At least, you need mention it in the text, and discuss these issues.

→ In the text, we mentioned this problem as follows: "We apply the same fixed thresholds (e.g., 3.4 and 10.4) for equations (6)-(7) as that in Chuine et al. (1999); however, we re-calibrate other parameters (e.g. T_c and C^*) so that these functions adapt to the phenological changes in U.S. deciduous forest." (Lines 268-271)

We discussed this issue as follows: "However, due to the data scarcity, all the selected sites are located in temperate areas ranging from 38°-46°N, suggesting that the model should be used cautiously at other latitudes and parameters may require re-calibration." (Lines 712-714)

P6046 L20, provide reference for the statement: temperature and photoperiod affects the autumn phenology.

 \rightarrow We have cited Delpierre et al. (2009) and Richardson et al. (2013) in the revised paper.

P6050 L5-13, the figure S3-S9, no RMSE, AIC and correlation coefficient values, better to show these values in a table S.

→ We have added a Table S5 to summarize those numbers.

P6050 L14-15, no model could predict the autumn phenology, i.e. correlation smaller than 0.5, how you conclude the temperature dominant the autumn phenology process?

→ We conclude that temperature dominates autumn phenology because simulations with and without photoperiod limit show similar results. However, as we discussed (refer to the responses to the general comments), this conclusion is model-dependent and is uncertain.

P6051 L18, you studied the country-scale, i.e. USA, no on the continental scale..

→ The scale of USA is large enough to be considered as continental scale. Similar definition could also seen in previous studies. For example, Schwartz and Hanes (2010) who investigated phenology for western U.S.

P6052 L11 the model-observation correlation -> the correlations between modeled and observed budburst dates. . .

→ Changed as suggested.

P6053 3.3 section, you should discuss the difference between the remote sensing based

phenology and the model results. . .

→ In section 3.3, we added a new remote sensing study from Buitenwerf et al. (2015) for comparison. The updated Figure 7 shows distributions of phenological changes even closer to our prediction (Figure 5) than the original results, further supporting our estimate of the phenological trends in U.S. using the well-calibrated model. We discussed differences between RS and simulations as follows:

"For U.S. forests, the longer growing season is primarily driven by later leaf-off dates, though regional advance of spring is also observed. Our results are generally consistent with their conclusions but with some deviations. For example, they observed later autumn in almost all the eastern U.S., where we predict delays only in the North and Northeast (Fig. 5b). Such discrepancies reflect prediction biases, and may also be a consequence of satellite retrieval uncertainties (Table 1)" (Lines 525-530)

"Our results show similar changes in spring phenology as the ensemble of the remote sensing studies, except that we predict smaller delays in the northern states (Fig. 5a). In addition, our data-informed model simulates significant spring advances in the central U.S., while remote sensing studies largely disagree over this area." (Lines 544-548)

P6055 3.4.2 section, please see the general comments.

→ We have carefully discussed the uncertainties in our conclusions about the impact of chilling and photoperiod.

P6057, the conclusion and discussion, it's kind of a 'Conclusion'... in the results section, you have a lot discussion, I would suggest to make a separate discussion section. . .

→ The similar comment has been proposed by the Reviewer #1 and we have changed "Conclusions and discussion" to "Conclusions" and added a separate "Discussion" section.

Table 1, the results, better providing the values of changes if you can, such as days per year or decade.

→ Reviewer #1 also proposed the similar comment. This is a good suggestion but might be difficult to implement for two reasons. First, regional phenological changes varied significantly across the U.S., while most of previous studies, if provided numeric values, show only numbers on the continental scale or for the latitude belts. For example, Jeong et al. (2011) reported almost zero changes in start of season over U.S. for 1982-1999. However, at the regional scale, this study showed both positive and negative trends in U.S. Second, the definition of phenological events varies among different studies (White et al., 2009) making it difficult to quantitatively perform the inter-comparison. As a result, we qualitatively compared phenological changes based on spatial maps from those

studies, so as to estimate the ensemble spatial distribution of phenological changes in the past decades.

Table 2, define the 'n' in the legend;

→ Defined it in a table footnote.

Table 3, the phenology dates are the average dates, right? Provide the std..

→ The regressed (now has changed the name to "LAI-derived" in Table 3) dates are based on one regression against all available records. As a result, there are no year-to-year values and standard deviations are not available. The modeled dates are based on interannually varied meteorology and the standard deviations have been shown in the revised Table 3.

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1 2	Probing the past 30-year phenology trend of U.S. deciduous forests
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Abstract

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Phenology is experiencing dramatic changes over deciduous forests in the U.S. Estimates of trends in phenology on the continental scale are uncertain, however, with studies failing to agree on both the magnitude and spatial distribution of trends in spring and autumn. This is due to the sparsity of in situ records, uncertainties associated with remote sensing data, and the regional focus of many studies. It has been suggested that reported trends are a result of recent temperature changes, though multiple processes are thought to be involved and the nature of the temperature forcing remains unknown. To date, no study has directly attributed long-term phenological trends to individual forcings across the U.S. through integrating observations with models. Here, we construct an extensive database of ground measurements of phenological events across the U.S., and use it to calibrate and evaluate a suite of phenology models. The models use variations of the accumulative temperature summation, with additional chilling requirements for spring phenology and photoperiod limitation for autumn. Including a chilling requirement or photoperiod limitation does not improve model performance, suggesting that temperature change, especially in spring and autumn, is likely the dominant driver of the observed trend during the past 3 decades. Our results show that phenological trends are not uniform over the contiguous U.S., with a significant advance of 0.34 day yr⁻¹ for the spring budburst in the East, a delay of 0.15 day yr⁻¹ for the autumn dormancy onset in the Northeast and West, but no evidence of change elsewhere. Relative to the 1980s, the growing season in the 2000s is extended by about 1 week (3-4%) in the East, New England, and the upper Rocky Mountains forests. Additional sensitivity tests show that intraspecific variations may not influence the predicted phenological trends. These results help reconcile conflicting reports of phenological trends in the literature, and directly attribute observed trends to long-term changes in temperature.

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Keywords: phenology, trend, interannual variability, deciduous forest, chilling requirement, growing season

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1 Introduction

Plant phenology, such as the timing of spring budburst and autumn leaf fall, is sensitive to temperature variation (Körner and Basler, 2010; Polgar and Primack, 2011; Richardson et al., 2013) and is thus exhibiting a long-term trend with the changing climate (Badeck et al., 2004; Cleland et al., 2007; Gordo and Sanz, 2009; Jeong et al., 2011). Long-term changes in phenology may be affecting ecosystem carbon assimilation (Keenan et al., 2014), surface water and energy balance (Schwartz and Crawford, 2001), and forest composition and evolution (Forrest and Miller-Rushing, 2010). Emerging observations have shown advanced spring and delayed autumn over the Northern Hemisphere, especially in Europe, during the past several decades (Menzel and Fabian, 1999; Fitter and Fitter, 2002; Menzel et al., 2006; Gordo and Sanz, 2009). However, the extent of regional phenological trends in U.S. remains uncertain as different studies present inconsistent and even opposite results (Table 1).

The uncertainty of the phenological changes in U.S. forests could be attributed to genetic, geographic, and temporal factors. First, experiments have suggested that different species may have different phenological sensitivity to temperature (Vitasse et al., 2009). Some species may also require cold temperatures before budburst (named chilling requirement). leading to divergent responses of U.S. plants to spring and winter warming at the community level (Cook et al., 2012) and the continental scale (Zhang et al., 2007). In addition, it is not clear whether other biotic and/or abiotic factors (e.g. humidity, photoperiod, tree age, and tree species) may play a role (Morin et al., 2009; Basler and Korner, 2012; Vitasse, 2013; Caldararu et al., 2014; Laube et al., 2014). Second, most deciduous forests in the U.S. are found at mid-latitudes, where temperature increases have not been uniform, and are not as strong as those at high latitudes (Hartmann et al., 2013). Third, differences in the time frames used in different studies may lead to apparently inconsistent trends (Badeck et al., 2004).

There are generally three approaches for estimating phenology at regional and continental scales: ground networks, remote sensing, and numerical modeling. Ground-based

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measurements can provide the most accurate phenological dates, such as budburst, flowering, and leaf fall. Some records last for decades and even centuries (Sparks and Menzel, 2002), making it possible to study long-term phenological change. However, such measurements usually have very limited spatial coverage. Ground-based networks, such as North American Lilac Network (Schwartz and Reiter, 2000), improve the spatial coverage but focuses only on 1-2 species, which may not represent the average phenological status of local plants. More extensive networks, such as the North American Phenology Network (www.usanpn.org) or the European Phenology Network (www.pep725.eu), contain many more species but typically do not have long data records (with some exceptions). Remote sensing provides a way to examine phenological changes over large scales but is inherently limited by short time scales or infrequent retrieval times and must be validated using ground measurements. Most of the recent estimates of phenological changes on the continental scale are performed using satellite retrievals (e.g., Zhang et al., 2007; Jeong et al., 2011; Piao et al., 2011). The lack of a universally accepted definition of phenological status for this method may lead to discrepancies up to 60 days for the timing of events among different algorithms and products (White et al., 2009). Moreover, date retrieval is often hampered, e.g., by cloud cover, which can lead to poor correlations with ground observations (Badeck et al., 2004; Schwartz and Hanes, 2010).

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Phenological models are useful tools for diagnosing causes of phenological changes and also for understanding the feedback of those changes to the Earth system (Richardson et al., 2013; Zhao et al., 2013). Evaluations of well-calibrated phenological models have shown high correlations between predictions and observations (e.g., White et al., 1997; Richardson et al., 2006; Delpierre et al., 2009; Vitasse et al., 2011). However, most of these state-of-art schemes are not evaluated at continental or even larger scales, thus limiting their applicability in dynamic vegetation models and climate models. Recent model-data comparisons have shown that the bias in the prediction of vegetation phenology is a large source of uncertainty in models of ecosystem carbon uptake (Richardson et al., 2012). This necessitates the development and evaluation of continental scale phenology models with continental scale observations.

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In this study, we use an extensive dataset of phenological observations to calibrate and evaluate 13 models (9 for spring and 4 for autumn) of deciduous tree phenology across the U.S. We first calibrate each model using derived phenological dates based on the long-term ground observations of Jeaf area index (LAI) at four deciduous forests. We then examine modeled interannual variability and trends, along with regional phenological differences, using an extensive network of phenological observations. The phenology model best supported by the observations is then applied to: (1) estimate the trend of both spring and autumn phenology of U.S. deciduous forests over the last three decades; (2) compare our results with other approaches (ground network, remote sensing, and model based) to identify robust changes and assess discrepancies; and (3) examine the underlying drivers of both the observed trends and interannual variability.

2 Materials and methods

We assembled and compared a suite of published models of spring and autumn phenology. Most of these models are built using cumulative thermal summations with constraining processes, such as chilling requirements and photoperiod limits. Model parameters were calibrated using long-term observations at four deciduous forest sites, with some model constants estimated based on literature values. An independent dataset of ground measurements was compiled and used to validate the performance of these models. In total, phenological observations from 1151 sites were used for model validation. In this section we first present the observations used for calibration and validation, followed by a description of the various model formulations tested and simulations performed.

2.1 Ground measurements for calibration

<u>Decadal</u> measurements of <u>LAI</u> from four U.S. deciduous broadleaf sites are collected

from the Ameriflux network (http://ameriflux.ornl.gov/) to calibrate parameters of the

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phenology model (Table 2<u>and Fig. 1</u>). We derive annual cycles of phenology by normalizing individual LAI values to the maximum and minimum LAI in each year for each site (Fig. S1, top panel). Since the measurements are discrete, we estimate the budburst dates (D1, marked on Fig. S1a), growing length (L1), offset start dates (D2), and falling length (L2) based on segmented regressions, which yield the minimum root mean square error (RMSE) against observations (Fig. S1 middle and bottom panel):

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$$RMSE = \sqrt{\frac{1}{n} \sum_{i=1}^{n} \left(O_i - P_i\right)^2} \tag{1}$$

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where O_i is the observation, P_i is the regression or prediction, and n is the number of samples. The measurements of LAI are not evenly distributed from year to year, and data at some years are too sparse to form the full annual cycle. As a result, we derive the decadal average phenological dates by regressing against all available LAI records at one site. The derived phenological dates are presented in Table 3. The average budburst date at US-MMS and US-MOz is earlier by three weeks than that at US-Ha1 and US-UMB, probably because the former sites are ~5 °C warmer than the latter. However, the start of leaf senescence is similar at all four sites, suggesting that photoperiod may also play an important role in regulating the autumn phenology, especially at the two warmer sites.

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2.2 Ground measurements for validation

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We use >75000 records for deciduous trees to evaluate the temporal variation and spatial distribution of simulated phenology (Table 4 and Table S1-S2). Data from three out of the four calibration sites (US-Ha1, US-UMB, US-MMS, Table 2 and Fig. 1) are also used for validation; however, we use them in different ways. For calibration, we use the decadal average phenology derived from the multiple-year LAI measurements, so that every calibrated model can capture the spatial pattern of phenology events on the continental scale. For validation, we use year-to-year phenological dates estimated from date records, photos, and LAI at each year, so as to identify the model that best captures the temporal variations. Most of the phenological records are discrete and evaluation of

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the annual cycle of tree phenology is difficult. Following definitions in earlier literatures (e.g., Zhu et al., 2012; Richardson et al., 2013), we validate spring budburst date (or the onset of growing season, the dates D1 in Fig. S1) and dormancy onset date (or the end of leaf fall period, the dates D2 plus falling length L2 in Fig. S1) from phenology models with the site-level records. The dormancy onset date defined here is based on the canopy level instead of the bud dormancy examined in a recent review paper by Delpierre et al. (2015).

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The two New England sites, Harvard Forest (http://harvardforest.fas.harvard.edu/) and Hubbard Brook (US-HB1) Forest (http://www.hubbardbrook.org/), have _decadal measurements back to 1990. The full records at Harvard Forest include 34 species, 16 of which are deciduous trees. The forest within the tower footprint is dominated by red oak (Quercus Rubra, 60% basal area), red maple (Acer Rubrum, 23% basal area), and secondary deciduous species. Hubbard Brook has three species, namely sugar maple (Acer Saccharum), American beech (Fagus Grandifolia), and yellow birch (Betula Alleghaniensis). We average over all trees and species at each site to generate average phenological dates for each year. Phenological observations are incomplete at two of the Ameriflux sites, US-UMB and US-MMS. We derive the missing phenological dates based on LAI data from Ameriflux and images from the PhenoCam project (http://phenocam.sr.unh.edu/webcam/). If the year-round LAI data are available at one site, we estimate budburst and dormancy start dates as the days when the interpolated or extrapolated LAI is equal to a selected threshold (see Supplement). Otherwise, we qualitatively estimate phenological dates based on photos from PhenoCam, which is a near-surface remote sensing network that observes phenology changes with highresolution digital cameras (Sonnentag et al., 2012). Based on the changes of tree color in these photos, we can easily identify the phase changes in phenology. For example, changes from gray to light green in spring could occur within several days. We select the middle of these few days as the budburst date. Similarly, changes from brown to gray in late autumn may happen within one week and the middle day of the week is selected as the dormancy onset date. An example of autumn dormancy at US-UMB is shown in Fig. S3. The dates derived from photos may have comparable precision as the observations

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from site-level phenological records (e.g., Fig. S2c), because the latter are also reported weekly or half-weekly.

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Data from ground networks was used to evaluate the model performance on the continental scale. The USA National Phenology Network (USA-NPN) is a nationwide project collecting standardized ground phenology observations by researchers, students, and volunteers. The network has limited records before 2009 but is significantly enriched thereafter. We select observations during 2011-2012 for 52 deciduous tree species that are most common in the U.S. (Table S1). The derived phenological dates for individual trees are averaged if they are observed at the same location (see Supplement). We also used observations from The North American Lilac Network (NALN), which provides records of the first leaf and first bloom dates of two lilac species, Common Lilac (Syringa Vulgaris) and Red Rothomagensis lilac (Syringa Chinensis), for the period of 1956-2003 (Schwartz and Reiter, 2000). As we shown in section 4.3, the phenology of individual species may vary by up to 3 weeks, however, the responses of phenology to temperature changes are relatively similar across species. We calculate correlations of budburst dates between observations and simulations at the available sites of NALN to validate the simulated temporal variations of phenology. We also adopt the limited long-term records from USA-NPN (Table S2) to evaluate the model over regions not covered by NALN.

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2.3 Spring phenology models

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Dozens of spring phenology models have been evaluated and inter-compared in the past two decades (Chuine et al., 1999; Linkosalo et al., 2008; Vitasse et al., 2011; Fu et al., 2012a; Fu et al., 2012b; Migliavacca et al., 2012; Melaas et al., 2013). These models may have different formats and parameters, but are generally dependent on temperature and photoperiod and could be divided into two categories, spring warming (or 1-phase) and chilling (or 2-phase), based on their assumptions of how warm and cold temperatures control the phenology development (Migliavacca et al., 2012). Although regional studies have demonstrated that the 1-phase models are as efficient as 2-phase models at the site level (e.g., Vitasse et al., 2011; Fu et al., 2012a; Migliavacca et al., 2012), we consider

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that chilling requirement may be necessary for the phenology at the continental and global scales where divergent phenological responses are observed (Zhang et al., 2007; Cook et al., 2012).

The chilling models have different formulations based on the sequences (sequential, parallel, or alternating) and forms (thermal summation or the Sarvas function) of chilling and forcing (Chuine et al., 1999). According to these differences, Migliavacca et al. (2012) summarized and compared eight models, listed as S1-S8 in Table 5, to fit phenology data at Harvard Forest. The sequential models require that a chilling threshold (C^*) must be achieved before the forcing (S_f) is effective. The parallel and alternating models calculate chilling units (S_c) and S_f at the same time, however, the increases in S_c can reduce the budburst threshold (F^*) for S_f following an exponential relationship $F^* = a \exp(b \times S_c)$. The functions of S_c and S_f are calculated as the cumulative thermal unit as follows:

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$$S_c(t) = \sum_{t_1}^t R_c(x_t)$$
 (2)

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$$S_f(t) = \sum_{t_2}^{t} R_f(x_t)$$
 (3)

where x_t is the daily temperature. The thermal unit may have two different formats. In the thermal summation approach (CF1, Equations 4 and 5), S_c is the number of chilling days (< T_c) from a starting day t_1 and S_f is the cumulative temperature higher than T_f (commonly named growing degree day, GDD) from day t_2 . In the other approach (CF2, Equations 6 and 7), both R_c and R_f are functions of daily temperature (Chuine et al., 1999).

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$$CF1: R_c(x_t) = \begin{cases} 0, & x_t \ge T_c \\ 1, & x_t < T_c \end{cases}$$
 (4)

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$$CF1: R_f(x_t) = \begin{cases} x_t - T_f, & x_t \ge T_f \\ 0, & x_t < T_f \end{cases}$$
 (5)

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$$CF2: R_c(x_t) = \begin{cases} 0, & x_t \le -3.4 \text{ or } x_t \ge 10.4 \\ \frac{x_t + 3.4}{T_c + 3.4}, & -3.4 < x_t < T_c \\ \frac{x_t - 10.4}{T_c - 10.4}, & T_c < x_t < 10.4 \end{cases}$$
 (6)

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$$CF2: R_f(x_t) = \begin{cases} 0, & x_t \le 0 \\ \frac{28.4}{1 + e^{-0.185(x_t - 18.4)}}, & x_t > 0 \end{cases}$$
 (7)

For both parallel and alternating models, t_1 is equal to t_2 , and for the latter, T_c is equal to T_f . For sequential models, t_2 is the first day when $S_c > C^*$. We apply the same fixed thresholds (e.g., 3.4 and 10.4) for equations (6)-(7) as that in Chuine et al. (1999); however, we re-calibrate other parameters (e.g. T_c and C^*) so that these functions adapt to the phenological changes in U.S. deciduous forest.

In a modified alternating scheme (S9), we decrease model complexity by fixing some parameters based on literature values. First, we fix t_1 as the winter solstice (December 22^{nd} in Northern Hemisphere, NH), after which photoperiod increases gradually. Second, we set T_c to 5°C, a value widely used for woody species (Murray et al., 1989; Kaduk and Heimann, 1996; Sitch et al., 2003). Third, we redefine the format of the forcing threshold as $F^* = a + b \exp(r \times S_c)$ following Murray et al. (1989) and set r=-0.01, a value used for temperate trees (e.g. beech and black locust). For each model in Table 5, we apply the exhaustive enumeration method to evaluate all combinations of the discrete parameters. We select the optimized parameters that jointly predict the lowest RMSE for the long-term budburst dates at the four calibration sites.

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We assume the green up process is linearly dependent on forcing S_f as follows,

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$$f_{S} = \begin{cases} 0, & S_{f} < F^{*} \\ \frac{S_{f} - F^{*}}{L_{g}}, & F^{*} \leq S_{f} \leq F^{*} + L_{g} \\ 1, & S_{f} > F^{*} + L_{g} \end{cases}$$

$$(8)$$

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where f_S is spring phenology ranging from 0 to 1. The parameter L_g is a growing length constraint calibrated based on the cycle of forest phenology (Fig. S1).

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2.4 Autumn phenology models

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Autumn phenology is more uncertain than budburst because it is affected by both temperature and photoperiod (Delpierre et al., 2009; Richardson et al., 2013). Three models have been developed to predict leaf fall with constraint from temperature and photoperiod, namely the continental phenology model by White et al. (1997), the growing season index (GSI) by Jolly et al. (2005) and the cold-degree day photoperioddependent model by Delpierre et al. (2009). The White et al. (1997) scheme is not compared in this study as it depends on soil temperature, which is not available at some sites. Jolly et al. (2005) calculated global phenology as the product of three segmented functions, which depend on the upper and lower limits in temperature (T_x and T_i), vapor pressure deficit (VPD) (V_x and V_i), and photoperiod (P_x and P_i), respectively. The value of VPD function is set to constant of 1 for temperate forests with no water stress. Delpierre et al. (2009) calculated the cumulative products of the functions of temperature and photoperiod. Those functions may have power indexes ranging from 0 to 2, suggesting that autumn phenology could be unrelated, linearly related, or exponentially related with the constraints from temperature and photoperiod. We calibrate all model parameters based on the observations at U.S. deciduous forests (A2-A3 in Table 5). We also use the original parameters from Jolly et al. (2005), which have been validated based on remote sensing data on the global scale (A1 in Table 5).

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 $\begin{aligned} \text{Deleted: } f_T = \begin{cases} 0, & S_f < I \\ \frac{S_f - F^*}{L_g}, & F^* \leq S_f \leq \\ 1, & S_f > F^* \end{cases} \end{aligned}$

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We also construct a simple scheme based on cumulative cold degree-days. The scheme, named 'CDD-photoperiod' (A4 in Table 5), calculates cold degree days (CDD) Ca following Richardson et al. (2006):

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$$C_a(t) = \sum_{t_3}^t R_a(x_t)$$
 (9)

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$$R_a(x_t) = \begin{cases} T_b - x_t, & x_t < T_b \\ 0, & x_t \ge T_b \end{cases}$$
 (10)

 where t_3 is the starting day set to summer solstice (June 22^{nd} in NH), and T_b is a base temperature of 20 °C as that in Dufrene et al. (2005) and Richardson et al. (2006). The leaf fall is triggered if C_a is higher than a threshold F_s and the length of falling period is determined by $L_{\rm f}$ as follows,

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$$f_{T} = \begin{cases} 0, & C_{a} \leq F_{s} \\ \frac{C_{a} - F_{s}}{L_{f}}, & F_{s} < C_{a} < F_{s} + L_{f} \\ 1, & C_{a} \geq F_{s} + L_{f} \end{cases}$$
 (11)

here f_T is the temperature-dependent phenology ranging from 0 to 1. We also define a photoperiod-limited phenology following Jolly et al. (2005),

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$$f_{P} = \begin{cases} 0, & P \leq P_{i} \\ \frac{P - P_{i}}{P_{x} - P_{i}}, & P_{i} < P < P_{x} \\ 1, & P \geq P_{x} \end{cases}$$
 (12)

where P is the daylength in minutes. P_i and P_x are the lower and upper limits of daylength during the period of leaf fall. Following Jolly et al. (2005), the final autumn phenology f_A of deciduous forest is determined as the product of f_T (Equation 11) and f_P (Equation 12).

2.5 Simulations

We perform both site-level and continental-scale simulations. For standalone simulations (simulation 1), phenology models are driven with daily surface air temperature sampled at each site (http://ameriflux.ornl.gov/). We gap-filled *in situ* temperature with daily reanalysis data from the Modern-Era Retrospective Analysis for Research and Applications (MERRA, Reichle et al., 2011; Rienecker et al., 2011), which is interpolated to each site based on the site location. The time span of each site-level simulation varies depending on the availability of the phenology observations. We perform a model intercomparison to determine which model is most supported by observations. The statistical metrics we used for evaluations include correlations, RMSE (Equation 1) and the Akaike Information Criterion (AIC), a measure of the trade-off between model predictability and model complexity (Akaike, 1973; Burnham and Anderson, 2002),

$$AIC = n \cdot \log \sigma^2 + 2p + \frac{2p(p+1)}{n-p-1}$$
 (13)

where *n* is the number of samples, *p* is the number of fit parameters for the model, and σ^2 is the square of RMSE between prediction and observations. A good prediction usually has high correlation coefficients but low RMSE and AIC values with observations.

For the regional simulation (simulation 2), we utilize daily surface air temperature from MERRA to drive the selected model on a resolution of 1° by latitude and 1.33° by longitude for 1982-2012. The uncertainty of predicted phenology is very sensitive to that of drivers (Migliavacca et al., 2012), as a result, we compare the MERRA forcing with ground observations from the United States Historical Climatology Network (USHCN, Easterling et al., 1996), which provides a high quality data set of daily and monthly

temperature from 1218 observing stations across the contiguous United States. We analyze the phenological trend for different time periods so as to understand how the selected time frame and interannual variability may influence our conclusions.

We, perform a sensitivity analysis (simulation 3) to evaluate the uncertainty due to phenological schemes. In this run, we do not include chilling constraint for the spring phenology by using a fixed and calibrated forcing threshold $F_{\mathbf{v}}^*$ of 50 degree days. As a result, forcing value $S_{\mathbf{f}}$ begins accumulation from winter solstice and budburst occurs if only $S_{\mathbf{f}} > F^*$. The whole process is not dependent on the value of chilling units $S_{\mathbf{c}}$. Meanwhile, we lift the photoperiod cap for leaf senescence by setting $f_{\mathbf{p}} = 1$, so that the autumn phenology is only determined by temperature ($f_A = f_T$).

We analyze species-specific temperature sensitivity of tree phenology at Harvard Forest (section 4.3). Based on these results, we perform two additional sensitivity tests to evaluate modeling uncertainties from the intraspecific variations. In the first run (simulation 4), phenological parameters are derived based on records of species with the lowest temperature sensitivity for both spring (Sweet Birch, *Betula Lenta*) and autumn (Paper Birch, *Betula Papyrifera*). In the other run (simulation 5), parameters are derived using records of species with the highest temperature sensitivity for spring (Striped Maple, *Acer Pensylvanicum*) and autumn (Black Oak, *Quercus Velutina*). We applied the derived parameters for the whole domain of U.S. by ignoring the realistic fractional coverage of specific species, so as to estimate the maximum uncertainty of prediction due to the intraspecific variations. We consider a change, trend, or correlation is significant if p < 0.05, unless otherwise stated.

3 Results

3.1.1 Site-level evaluation

3.1 Model evaluation

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The five sites we select to calibrate and evaluate models are all located at Eastern U.S., where >90% deciduous forests are located (Fig. 1). The site-level evaluations for 9 spring models and 4 autumn models are shown in Fig. 2 and summarized in Table S5. For the spring phenology, the alternating approach (S7-S9) has higher correlations and lower RMSE compared to parallel models (S3-S6). The sequential approach with thermal summation (S1) shows the largest correlations and lowest biases. However, it requires fitting 5 parameters, increasing its AIC value relative to the alternating models. The three alternating models have comparable correlations and RMSE. However, the modified alternating model (S9) has the lowest AIC, suggesting that fixing some parameters based on literature does not weaken the performance but can reduce model complexity. For the autumn phenology, no models predict correlations higher than 0.5, indicating that missing mechanisms, such as accidental frost, strong wind and rainfall, may be required to improve the current model structures (Richardson et al., 2006; Schuster et al., 2014). The 'CDD-photoperiod' scheme (A4) has comparable performance with that from Delpierre et al. (2009) (A3) based on correlation and RMSE, and has lower AIC than the latter due to the lower number of fit parameters (Table 5). As a result of the site-level evaluations, we select the spring model S9 and autumn model A4 (parameters listed in Table S3) as the state-of-art schemes for the regional simulations.

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470 471 Site-level simulations with models S9 and A4 capture both the interannual variations and temporal trends of phenology at the validation sites (Fig. 1). Sites US-Ha1 and US-HB1 provide >20 years of phenology records. The observation-simulation correlations for budburst dates are 0.7-0.8 at these sites. Model performance is poor for autumn phenology, with correlation coefficients between 0.2-0.4. Both observed and predicted budburst dates at US-Ha1 show significant advances of ~0.5 day yr⁻¹ during 1992-2012. However, at US-HB1, the observed trend of -0.3 day yr⁻¹ is not significant due to large interannual variations. In contrast, the dormancy start dates remains almost constant at

US-Ha1, similar as that reported by Lee et al. (2003), but exhibits a significant delay of ~0.5 day yr⁻¹ at US-HB1 in the past two decades, as reported by Keenan et al. (2014).

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Sites US-UMB and US-MMS have relatively short observations for 1999-2012. Missing *in situ* forcing values limit the model's spring phenology performance compared to that using MERRA reanalysis. With MERRA forcing, the model shows high correlations (~0.8) and low biases (2-4 days) in the prediction of budburst dates. The simulated autumn phenology again has lower correlations with observations at these sites. The predicted dormancy start dates at US-UMB match the observed interannual variation before 2010 but fail to capture the perturbations thereafter. The prediction at US-MMS shows similar year-to-year variations as observations but with smaller magnitude. The spring budburst dates show moderate changes at US-UMB but a significant advance at US-MMS in the past decade. For the autumn phenology, both observations and simulations show insignificant changes.

3.1.2 Continental-scale evaluation

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Phenology has a distinctive spatial distribution over U.S. deciduous forests (Fig. 3). Budburst occurs relatively later in the west of 105°W but earlier in the low latitudes of the East (Fig. 3a). The area-weighted (based on cover fraction of deciduous forest) budburst date for the western U.S. is May 4th or the 124th day of the year (DOY), with higher values of > DOY 140 over the ridge of Rocky Mountains. In contrast, the mean budburst date is April 15th (DOY 105) for the east of 105°W, with even earlier dates of <DOY 100 at south of 40°N. At higher latitudes, such as the forests over New England and Great Lakes, spring usually begins after DOY 125, due to the colder spring temperatures. The simulated spatial pattern is consistent with phenology records from the USA-NPN network, with a correlation coefficient of 0.77 over 46 sites (Fig. 3b). However, the predicted budburst date at these sites is 5 days on average later than the observations. Causes of such bias are unclear but might be related to the uneven spatial distribution of network sites, the distinct nature of the protocols between calibration and validation data, and the incompatibility between model parameters derived at regional scale versus those for the continental scale. The distribution of autumn phenology shows almost opposite pattern as that of spring phenology (Fig. 3c). At high latitudes and/or altitudes, autumn phenology is sensitive to cold temperatures and as a result exhibits an

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early dormancy onset. The validation against observations from 23 USA-NPN sites yields a significant correlation coefficient of 0.80 for the simulated autumn phenology (Fig. 3d). Similar to the spring budburst, predicted dormancy onset is later by 11 days than the observations. The S9 model also reproduces year-to-year changes in spring phenology. In 2011, the area-weighted budburst date is DOY 117 (Fig. S12), which is advanced by 13 days in 2012 (Fig. S13). Such change follows the continental warming of spring (March-May) temperature by ~3 °C in the latter year (not shown).

We further evaluate the simulated year-to-year budburst dates with available long-term records from NALN and USA-NPN network (Fig. 4). The correlations between modeled and observed budburst dates are Jarger than 0.3 for 47 out of 59 sites, among which 26 are significant (p<0,1), suggesting that the predicted interannual variation and long-term trend of spring phenology are generally reasonable on the continental scale. The insignificant correlations at 33 sites are in part attributed to the deviations in species between model (PFT level) and measurements (species level). Furthermore, the record length may also contribute to these biases because 28 out of the 33 sites with insignificant correlations have records shorter than 8 years. The large interannual variability in the spring phenology (see section 4.1) may affect the correlations especially for time series with short record length. On the other hand, no long-term records are available to evaluate the temporal variation of simulated autumn phenology on the continental scale.

3.2 Phenological change in U.S. deciduous forests

Driven with the MERRA forcing, the model simulates a significant advance of spring budburst dates in central eastern U.S. during 1982-2012 (Fig. 5a). The largest advance of 0.42 day yr⁻¹ is predicted in the states of Illinois and Indiana. For eastern states covered with >50% deciduous forests, such as Pennsylvania, West Virginia, and Virginia, the budburst date is advanced by 0.34 day yr⁻¹. However, for deciduous forests in the western, northern, northeastern, and southeastern U.S., the changes are either small or insignificant. Two New England sites, Harvard Forest and Hubbard Brook, are located within the same region but have different trends of spring phenology (Fig. 5a), consistent

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with site-level evaluations for 1992-2012 (Fig. 1). On the other hand, the dormancy start date is delayed by 0.20 day yr⁻¹ in the northern (Minnesota), 0.14 day yr⁻¹ in the northeastern, and 0.16 day yr⁻¹ in the western forests (Fig. 5b). However, the autumn phenology in central and southern U.S. does not show significant changes, consistent with site-level evaluations at US-UMB and US-MMS (Fig. 1).

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> The spatial pattern of the trend in forest phenology follows spatial patterns of temperature changes in the past 3 decades (Fig. \$14). Both the reanalysis data and ground records show a significant spring warming of 0.75 °C decade⁻¹ over central and eastern U.S. while insignificant changes in the other portion of deciduous forest (Figs. \$14c-d). Meanwhile, the warmer winter may delay the spring budburst by reducing chilling days, especially for forest in the northern U.S (Figs. \$14a-b). On the other hand, autumn warming in the northern, northeastern, and western forests (Figs. \$14e-f) results in delayed dormancy dates in those regions (Fig. 5b). However, autumn phenology in central, eastern, and southern forests shows no significant change, due to either moderate changes in temperature (Figs. \$14e-f) or regulation through photoperiod. Based on the synchronous phenological responses to temperature changes, we estimate long-term temperature sensitivities of -3.3 days °C⁻¹ for spring budburst date and 2.2 days °C⁻¹ for dormancy start date over U.S. deciduous forests. These values are close to the estimates of -2.8 ± 0.3 days °C⁻¹ (spring) and 1.8 ± 0.8 days °C⁻¹ (autumn) based on observations from five U.S. deciduous sites (Keenan et al., 2014). The temperature sensitivity of spring budburst date is also within the range from -2.05 to -7.48 days °C⁻¹ for different species based on the field experiments performed by Vitasse et al. (2009).

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Advanced spring and delayed autumn together increased the length of the growing season across the U.S. (Fig. 6). Relative to the 1980s, the growing season in the 2000s extends by 5.5 days (3.0%) in the eastern states with dense forest coverage (fraction > 50%). The model predicts larger extension of 6.4 days (3.9%) in New England, 7.0 days (3.6%) in states Illinois and Indiana, and 6.0 days (4.3%) in the upper Rocky Mountains forests (Fig. 6). This magnitude is comparable to the trend of 2.1-4.2 days per decade in Eurasian

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and North American temperate forest estimated by other studies (Menzel et al., 2008; Jeong et al., 2011).

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3.3 Comparison with results from remote sensing

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Most of up-to-date estimates of the changes in U.S. forest phenology are performed with remote sensing data. In a recent study, Buitenwerf et al. (2015) found an overall extension of the growing season over boreal and temperate forests during 1981-2012 based on the Normalized Difference Vegetation Index (NDVI) from satellite data. However, the exact phenological changes that underlie such overall greening differ among regions. For U.S. forests, the longer growing season is primarily driven by later leaf-off dates, though regional advance of spring is also observed. Our results are generally consistent with their conclusions but with some deviations. For example, they observed later autumn in almost all the eastern U.S., where we predict delays only in the North and Northeast (Fig. 5b). Such discrepancies reflect prediction biases, and may also be a consequence of satellite retrieval uncertainties (Table 1).

We <u>further</u> compare our results to recent reports from the literature, selecting all studies that <u>examine</u> phenological trends across the U.S. for at least 20 years (Table 1). All selected studies use the <u>NDVI</u>, however, they report different and even opposite trends. Such discrepancies may be attributed to the differences in the definitions of phenological dates (White et al., 2009) or the statistical algorithms in the extraction of the dates (Keenan et al., 2014). Here, we summarize their results on Fig. <u>7</u> so as to conclude the most robust changes for U.S. forest phenology in the past 2-3 decades. <u>Since the definition of phenological events varies among different studies (White et al., 2009)</u>, we <u>qualitatively compare the simulations with the remote sensing retrievals so as to evaluate the ensemble spatial distribution of phenological changes in the past decades. For spring phenology, <u>four out of seven studies predict advanced budburst or greenup dates in the East, while four predict delayed dates in the North (Fig. <u>7a)</u>. There are no evident phenological changes in spring phenology as the ensemble of the remote sensing studies, except that</u></u>

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3.4 Modeling uncertainties

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we predict smaller delays in the northern states (Fig. 5a). In addition, our data-informed model simulates significant spring advances in the central U.S., while remote sensing studies largely disagree over this area. On the other hand, both the remote sensing studies and our results show that autumn phenology is significantly delayed in the West, North, and Northeast (Figs. 5b and 7b). However, the examined studies also exhibit significant delays in the central states, in contrast to our results. In other areas, the trends are insignificant (Southeast and East).

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4. Discussion

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4.1 Impact of interannual variability

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Estimates of trends in phenology are sensitive to the length of the examined time frame due to relatively large internal climate variability (Badeck et al., 2004; Iler et al., 2013). Our analyses show that interannual variations may also cause large uncertainties in the estimated phenology trend, especially on short decadal time scales. For example, Keenan et al. (2014) estimated a large advance of 0.48 day yr⁻¹ in the spring phenology in both the Harvard Forest and Hubbard Brook sites between 1990 and 2012, and across the Eastern U.S. temperate forest for 2000-2012. Our data-informed modeling approach estimated a similar change of 0.42 day yr⁻¹ between 2000 and 2012 over the eastern US (Fig. \$15a), but the trend was largely affected by the record-breaking advance of spring in 2012 (Jolly et al., 2005), especially over the central and eastern states (Figs. S12-S13). If we exclude this specific year, we achieve an average trend of only -0.05 day yr⁻¹ for 2000-2011, with delayed budburst dates in central and southern states (Fig. \$15b). In addition, interannual variability may affect the significance of the derived trend. As shown in Fig. \$15a, the advance of spring phenology is not significant for 2000-2012, based on the linear regression, possibly because of the large year-to-year variations and the insignificant changes in air temperature (Fig. \$16). A similar result is shown for autumn phenology (Fig. \$15d). However, if we extend the analysis period to 1982-2011, the estimated trends and their significance are not affected by the anomalous phenology

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change in the year 2012 (Figs. \$15c and \$15f), suggesting that the estimate of long-term trend is more robust compared to the short-term trend.

4.2 Impact of chilling requirement and photoperiod limit

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We perform an additional sensitivity experiment (simulation 3) to examine the impact of model structure on the phenology prediction. For spring phenology, model validations have shown that the spring warming (1-phase) models are as efficient as chilling (2phase) models (Vitasse et al., 2011; Fu et al., 2012a; Migliavacca et al., 2012). In the simulation 3, we remove the limit of chilling requirement on the forcing threshold F^* by defining a fixed forcing threshold. The site-level evaluation shows that this simulation has higher correlations at three out of four sites compared to that with chilling requirement (not shown). Driven with MERRA temperature, the simulation 3 (Fig. \$17a) predicts a similar spatial pattern for the trend of budburst date in the U.S. as that in simulation 2 (Fig. 5a), although the former estimates larger advances in central (0.52 day yr⁻¹) and eastern U.S (0.43 day yr⁻¹). Such stronger signal in the trend of spring phenology could be attributed to the omission of offset effects from the winter warming (Figs. \$14a-b). In the simulation 3, we also remove the cap of photoperiod for autumn dormancy and achieve better correlations between simulations and observations at all sites, though this method tends to generate later dormancy, especially at warm sites (up to 20 days, not shown). Continental-scale simulation without photoperiod limit (Fig. \$17b) results in similar trend in autumn phenology as that with photoperiod (Fig. 5b), suggesting that the response to temperature dominates the phenological change in the U.S. deciduous forest.

Our investigation of the roles of chilling and photoperiod is sensitive to the model structure, climate variability, and data availability. First, the similar performance between spring warming and chilling models might also result from the inaccurate representation of chilling / photoperiod mechanisms. For example, the chilling units used in our parameterization are calculated based on daily average temperatures, while Piao et al. (2015) suggested that leaf unfolding dates during 1982-2011 are triggered by daytime

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more than by nighttime temperature. The up-to-date autumn phenology model fails to capture interannual variability of dormancy onset (Fig. 2), suggesting that unknown processes are involved in the autumn leaf fall (Keenan and Richardson, 2015). It is unclear whether these processes are related to the variations of photoperiod. Second, the decadal changes in temperature may mask the role of chilling. The trend of winter warming is not significant for most areas in the U.S. (Fig. S14a), suggesting that chilling requirements have been fulfilled in the past 3 decades. However, it is unclear whether the winter warming will intensify in the future, which may slow the advancement of spring budburst. Third, we choose to calibrate the phenological parameterization at the level of plant functional type (PFT) because species-specific measurements are usually incomplete in time and uneven in space. Such incompleteness may influence the accuracy of derived decadal phenological records used for both model calibration and validation. At the same time, PFT-level parameterization may be too broad for the vegetation modeling because it fails to capture intraspecific variations (Van Bodegom et al., 2012; Reichstein et al., 2014). Observations at the community level suggest that the budburst of some species is sensitive to fall/winter and spring warming but with opposite signs (Cook et al., 2012). In the next subsection, we examine the records of 13 deciduous tree species at Harvard Forest.

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4.3 Impact of species aggregation

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Tree phenology and its responses to temperature changes <u>have been shown</u> to vary among species (Vitasse et al., 2009; Fu et al., 2012a; <u>Archetti et al., 2013</u>). In this study, however, we calibrate model parameters based on the long-term phenological cycle derived from LAI, which represents the mean growing seasonality averaged among species. We do not perform the species-specific simulation for the following three reasons. First, the species-level measurements are usually not available on the continental scale, which influences both model calibration and validation. Second, species-level modeling increases the complexity and computational costs while decreasing predictive reliability (Prentice et al., 2015). Third, investigations at both site level and continental

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scale show similar temperature sensitivity of tree phenology between the species-specific and species-aggregation approaches.

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We analyze the temperature sensitivity of tree phenology for 13 DBF species at Harvard Forest (Fig. 3). We calculate the ensemble phenology based on the basal area of each species (the dominant species are red oak (Quercus Rubra, 60% basal area) and red maple (Acer Rubrum, 23% basal area)) in order to represent the average phenology at Harvard Forest, which has been used in the site-level evaluation (Fig. 1). For spring phenology, the mean budburst dates vary by up to 3 weeks among different species, with the earliest being alternated-leaved dogwood (Cornus Alterniflora) and the latest white oak (Quercus Alba) (Fig. &c). Two dominant species, red oak and red maple, have similar year-to-year variations, leading to a similar magnitude of ensemble phenology and the long-term trend (Fig. 8a). The 21-year average of the ensemble budburst date is DOY 126, very close to the DOY 125 derived from LAI (Table 3). Regressions against mean March and April temperature show similar sensitivity of budburst date for most species, especially for red oak (-3.8 day °C⁻¹) and read maple (-3.4 day °C⁻¹) (Fig. &c). Such similarity also provides us the foundation to validate the simulated interannual variation of spring phenology with the lilac data (Fig. 4). For autumn phenology, the averaged dormancy onset date of red maple is 23 days earlier than that of red oak (Fig. 8d), leading to medium ensemble values (Fig. 8b). The 21-year average of the ensemble dormancy onset date is DOY 306, again close to the estimate of DOY 310 based on LAI (Table 3). The temperature sensitivity of autumn phenology is positive for all species, including similar magnitude of 2.6 day °C⁻¹ for red maple and 2.3 day °C⁻¹ for red oak (Fig. §f), though the latter is insignificant due to the large year-to-year variations. The speciesspecific analyses show that calibration based on LAI may capture the representative phenology at deciduous forests, and is not affected by the large deviations among species. Since U.S. is dominated oak (http://www.nrs.fs.fed.us/atlas/tree/curr fortypes.html), which we show have very similar temperature sensitivity for both the spring and autumn phenology, we expect that the species aggregation applied in this study may reasonably capture the temperature

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sensitivity of forest phenology on the continental scale, given that temperature is likely the dominant driver of phenology change for such deciduous forests (Fig. 5).

We perform two sensitivity runs to evaluate the modeling uncertainties due to intraspecific variations at the continental scale (Fig. S18). Simulations with either the lowest (simulation 4) or the highest (simulation 5) temperature sensitivity yield very similar phenological trends as that in the control simulation (simulation 2). In the East, simulation 4 predicts a spring advance by 0.33 day yr⁻¹ while simulation 5 predicts an advance by 0.35 day yr⁻¹, both of which are close to the 0.34 day yr⁻¹ from the control run. In the West and Northeast, both sensitivity runs predict autumn delay by 0.13-0.15 day yr⁻¹, lower than value of 0.14-0.16 day yr⁻¹ from control run, suggesting that site-level responses may not be necessarily consistent with responses at the continental scale. Both the similar temperature sensitivity at site level (Fig. 8) and the predicted phenological trends at continental scale (Fig. S18) support the concept of phenological modeling at the forest and PFT level, and corroborates the further investigation of phenology-climate interactions at the continental and global scale.

5 Conclusions

 We performed model inter-comparison to identify the state-of-art scheme for predicting tree phenology of U.S. deciduous forests. An extensive database of ground measurements, including long-term records of phenological events at the site level and short-term records widely scattered on the national scale, was compiled to evaluate the models. The selected models with the lowest AIC values utilized the accumulative temperature summation, with additional constraints of winter chilling on spring phenology and photoperiod on autumn phenology. The 30-year phenology trend of U.S. deciduous forest was explored using the selected models. Consistent with an ensemble of remote-sensing studies, the continental simulation showed a significant advance of 0.34 day yr⁻¹ for spring budburst dates in the East with >50% coverage of deciduous forests during 1982-2012. However, no significant changes were found over the western,

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northern, northeastern, and southeastern U.S. On the other hand, the autumn dormancy onset dates is delayed by 0.20 day yr⁻¹ in the northern, 0.14 day yr⁻¹ in the northeastern, and 0.16 day yr⁻¹ in the western forests, but is not significant elsewhere.

Uncertainties in phenological predictions originate from drivers, parameters, and model structures (Migliavacca et al., 2012). In this study, we minimize uncertainties from meteorological forcings by utilizing an updated reanalysis product and validate the gridded forcings with site-based observations. For the model parameters, we calibrate model parameters with long-term average phenology at four deciduous sites with diverse spatial distribution. This approach was chosen because a well-calibrated phenology model based on a single dataset may have poor performance against external data sets (Chuine et al., 1999; Richardson et al., 2006). The validation shows that the predicted spatial pattern is reasonable and the long-term average matches observations within sampling uncertainty (Figs. 3-4). However, due to the data scarcity, all the selected sites are located in temperate areas ranging from 38°-46°N, suggesting that the model should be used cautiously at other latitudes and parameters may require re-calibration. For model structure, we perform sensitivity tests both with and without chilling requirements and photoperiod limit and find that the predicted phenology and its change is not sensitive to these constraints at least for the U.S. domain.

Our model inter-comparison does not show a distinct advantage for a specific spring model, suggesting that the model formulation, such as sequential, parallel, and alternating, is not a dominant source of uncertainty for estimates of spring phenology. On the other hand, the evaluation of autumn phenology shows that models with cumulative cold summation and photoperiod limits may better capture the trend of the dormancy onset dates. However, the state-of-art autumn models still have large biases in capturing year-to-year variations. Missing mechanisms, potentially including biotic (e.g. tree age (Vitasse, 2013; Caldararu et al., 2014) and species (Vitasse et al., 2009)) and abiotic (e.g. water stress (Jones et al., 2014), accidental frost (Schuster et al., 2014), strong wind, and air pollution (Gallinat et al., 2015), and timing of spring flushing (Fu et al., 2014; Keenan

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and <u>Richardson</u>, 2015)) factors, may jointly affect leaf fall in a process that is currently not well understood.

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Given these uncertainties, our results show a significant advance of 0.34 day yr⁻¹ for spring budburst dates in the East of U.S. during 1982-2012, while a delay of 0.15 day yr⁻¹ for autumn dormancy onset dates in the Northeast and West. Such long-term changes in phenology are mainly attributed to the trends in temperature, as simulations without chilling requirement and photoperiod limit showed similar phenological changes. Due to either the advances in spring or delays in autumn, tree growth period extends by about 1 week (3-4%) at the 2000s relative to the 1980s, indicating prominent influences of climate change on the carbon cycle and ecological evolution of the U.S. deciduous forests.

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Table 1. Summary of studies estimating phenology trend in U.S. for at least 20 years.

	Studies	Period	Data sets	Results					
A	Reed (2006)	1982-2003	NDVI (AVHRR)	Spring: scattered trends towards advance and delay. Autumn: significant delay in the Northeast and Northwest	Xu Yue 7/2/15 11:18 AM Deleted:				
В	Zhang et al. (2007)	1982-2005	NDVI (AVHRR)	Spring : advance in Center and East but delay in the North and Southeast.	Xu Yue 7/2/15 11:18 AM Deleted: Zhang et al. (2007)				
C	Julien and Sobrino (2009)	1981-2003	NDVI (GIMMS)	Spring: advance in the West and East, no trend in the Northeast and Southeast, delay in the North. Autumn: advance almost everywhere.					
D	White et al. (2009)	1982-2006	NDVI (AVHRR)	Spring : no evidence for time trends for most areas v significant delay in the North.	vith				
Е	Jeong et al. (2011)	1982-2008	NDVI (AVHRR)	Spring : no evidence for time trends for most areas. Autumn : delay in the West, North, Northeast, and Southeast (except Center).					
F	Dragoni and Rahman (2012)	1989-2008	NDVI (AVHRR)	Autumn : significant delay in Northeast but insignificanges in the East and North	cant				
G	Zhu et al. (2012)	1982-2006	NDVI (GIMMS)	Spring: significant delay in the Center and East: Autumn: significant delay in the West but almost no changes in the East	Xu Yue 7/2/15 11:18 AM Formatted Table				
<u>H</u>	Buitenwerf et al. (2015)	<u>1981-2012</u>	NDVI (GIMMS)	Spring: advance in the East and Southeast, but almono changes in Northeast, North, and West. Autumn: delay in the East, Southeast, Northeast, an North, but almost no changes in the West.					
1172									
1173	1173 NDVI: Normalized Difference Vegetation Index								

AVHRR: Advanced Very High-Resolution Radiometers

GIMMS: Global Inventory Mapping and Monitoring Studies

Table 2. Ground measurements of leaf area index (LAI) used to calibrate the phenology model. The location of these sites is denoted on Fig. 1.

- 1	1	Q	6

\$ite	Name	Latitude	Longitude	Years	n_a	Reference
US-Ha1	Harvard Forest	42.54°N	72.17°W	1998-2008	68	Urbanski et al. (2007)
US-UMB	Univ. of Michigan Biological Station	45.56°N	84.71°W	1999-2007	116	Gough et al. (2008)
US-MMS	Morgan Monroe State Forest	39.32°N	86.41°W	1999-2010	207	Schmid et al. (2000)
US-MOz	Missouri Ozark	38.74°N	92.2°W	2006-2012	149	Gu et al. (2006)

 $\frac{a}{n}$ denotes the number of records

1	192
1	193
1	194

1195 1196 Table 3. Phenological and climatological parameters for four deciduous forest sites 1197 predicted by segmented regressions (Fig. S1) and the selected phenology models (S9+A4, 1198 refer to Table 5).

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	Sites	Annual	Budl	ourst	Grow	length	Offse	et start	Offset	length	
		Temp	(day o	f year)	(da	ys)	(day o	of year)	(da	. (3)	ı Yue 7/2/15 11:18 AM
		(°C)	LAI-	Model	LAI-	Model	LAI-	Model	LAI-	Mode.	ormatted Table
			derived		derived		derived		derived		ı Yue 7/2/15 11:18 AM
U	S-Ha1	8.0	125	122 ± 5	30	47 <u>±7</u>	271	270 ± 10	39	33 #	eleted: Reg.
	•										ı Yue 7/2/15 11:18 AM
U	S-UMB	7.2	124	125 ± 4	42	45 <u>±5</u>	273	265 ± 21	34	.54 ±\ ==	eleted: Reg.
										Χι	ı Yue 7/2/15 11:18 AM
US	S-MMS	12.3	100	103 ± 5	51	39 <u>±4</u>	276	275 ± 6	35	4() +	eleted: Reg.
	7						_, ,			Χι	ı Yue 7/2/15 11:18 AM
II	S-MOz	13.3	103	102 ± 4	41	35 ± 3	270	275 ± 5	45	42 ± D	eleted: Reg.
	,OZ	13.3	105	102		33 <u>+ 3</u>	270	273 = 3			

Table 4. Ground phenology measurements of deciduous trees used to validate the model.

Site / network	Category	Duration	Sites	Species	Trees	n	Reference / Link
Harvard Forest	Dates	1990-2012	1	16	56	32393	O'Keefe (2000)
Hubbard Brook	Dates	1989-2012	1	3	27	1081	Bailey (2014)
	LAI	1999-2012	1	N/A	N/A	171	http://ameriflux.ornl.gov/
US-UMB	Dates	1999-2012	1	5	66	259	Gough et al. (2008)
	Photos	2005-2012	1	N/A	N/A	1265	Sonnentag et al. (2012)
	LAI	1999-2012	1	N/A	N/A	207	http://ameriflux.ornl.gov/
US-MMS	Dates	2000-2004	1	N/A	N/A	4	http://ameriflux.ornl.gov/
	Photos	2008-2012	1	N/A	N/A	1480	Sonnentag et al. (2012)
National Phenology Network 1 ^a	Dates	2011-2012	588	52	1986	29280	https://www.usanpn.org/
National Phenology Network 2 ^b	Dates	2004-2012	167	7	195	4231	https://www.usanpn.org/
North American Lilac Network	Dates	1982-2003	392	2	N/A	5072	Schwartz and Reiter (2000)

^a Data used to evaluate spatial distribution of simulated phenology. Detailed species

information is listed in Table S1.

^{1217 &}lt;sup>b</sup> Data used to evaluate temporal variation of simulated phenology. Detailed species 1218 information is listed in Table S2.

1224
1225 **Table 5.** Summary of phenology models with fit parameters calibrated against the long1226 term phenology at four U.S. deciduous sites. The detailed parameters for the selected
1227 models, S9 and A4, are summarized in Table S3. Optimized parameters for other models
1228 are summarized in Table S4.

ID	Model Name	Category	Fixed Parameters	Fit Parameters
S1	Sequential CF1	Spring	0	$5(t_1, T_f, T_c, C^*, F^*)$
S2	Sequential CF2	Spring	0	$4(t_1, T_c, C^*, F^*)$
S3	Parallel1 CF1	Spring	0	$6(t_1, T_f, T_c, C^*, a, b)$
S4	Parallel1 CF2	Spring	0	$5(t_1, T_c, C^*, a, b)$
S5	Parallel2 CF1	Spring	0	6 $(t_1, T_f, T_c, C^*, a, b); t_2 = t_1$
S6	Parallel2 CF2	Spring	0	$5(t_1, T_c, C^*, a, b); t_2 = t_1$
S7	Alternating CF1	Spring	0	$4(t_1, T_c, a, b); T_f = T_c; t_2 = t_1$
S8	Alternating CF1 t1 fixed	Spring	$1(t_1)$	$3 (T_c, a, b); T_f = T_c; t_2 = t_1$
S9	Alternating CF1 modified	Spring	$3(t_1, T_c, r)$	2 (a, b); $T_f = T_c$; $t_2 = t_1$
A 1	Jolly-2005 Origin	Autumn	$4(T_{i}, T_{x}, P_{i}, P_{x})$	0
A2	Jolly-2005 Adjusted	Autumn	0	$4(T_{i}, T_{x}, P_{i}, P_{x})$
A3	Delpierre-2009	Autumn	0	$6 (P_{\text{start}}, T_{\text{b}}, x, y, Y_{\text{crit}}, L_{\text{f}})$
A4	CDD-photoperiod	Autumn	$2(t_3, T_b)$	$4(F_{\rm s},L_{\rm f},P_{\rm i},P_{\rm x})$
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Figure captions

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Figure 1. Simulation of spring and autumn phenology at four U.S. deciduous broadleaf forest (DBF) sites. The map shows the fraction of U.S. DBF derived from the Advanced Very High Resolution Radiometer (AVHRR). The area with >3% coverage is the domain for this study. Five triangles indicate the locations of sites whose long-term measurements of meteorology and phenology are used for the calibration and/or validation of the model: Harvard Forest (US-Ha1), Hubbard Brook Forest (US-HB1), Morgan-Monroe State Forest (US-MMS), University of Michigan Biological Station Forest (US-UMB), and Missouri Ozark Forest (US-MOz). Phenological dates are recorded at US-Ha1 and US-HB1 during 1992-2012. Measurements of leaf area index (LAI) and photos are used to derive phenology at US-UMB and US-MMS for 1999-2012. Derived phenological dates at US-MOz are used for model calibration but not validation and are not shown here. At each site, two simulations are performed with the spring model S9 and autumn model A4 (refer to Figure 2), driven by temperatures from either the in situ measurements (blue) or the Modern Era Retrospective-Analysis (MERRA) reanalysis (green). Trend of each time series (units: day yr-1) is shown with colors indicating results from observations (red) and simulations (blue or green). Significant trends (p<0.05) are marked with asterisks.

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Fig. 2_xComparison of model performance in the prediction of phenological dates at four U.S. DBF sites among (top) nine spring phenology models and (bottom) four autumn phenology models. The statistical metrics are correlation coefficient, root-mean-square error_x (RMSE), and the Akaike Information Criterion_x (AIC). Each point represents the mean values of the statistical metrics at four sites for one model. The error bar represents the range of the metrics. Each model uses the optimized parameters as summarized in Table 5 for the prediction. The red ones are the models used for the continental predictions. Detailed predictions at each site are shown in Figs. S4-S11. The values of correlation coefficients, RMSE, and AIC are summarized in Table S5.

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Figure 3. Comparison of the simulated (a, b) budburst and (c, d) dormancy dates with *in situ* observations (colored circles) from the USA National Phenology Network for 2011-2012. Simulations are performed with the spring model S9 and autumn model A4. The number of the sites and the correlation coefficients are shown in the scatter plots. The separate evaluations in 2011 and 2012 are shown in Figs. S12 and S13. The coverage of colored patches in (a) and (c) differs from that in Figure 1 because values at and beyond the low end of color scales have been shown in white. The number of the sites and the correlation coefficients are shown in the scatter plots. The number of sites shown in the plot is much fewer than the total of 588 because only a small portion of the sites has continuous records for both years and a stringent screening process is applied to derive phenological dates (see Supplement). The separate evaluations in 2011 and 2012 are shown in Figs. S12-S13.

Figure 4. Correlations (circles) between the predicted budburst dates and observed first-bloom dates from the North American Lilac Network (circle) and first-leaf dates from the USA National Phenology Network (squares). Simulations are performed with the spring model S9. The correlation coefficients are calculated for individual trees with at least 6 years of observations during 1982-2012. Correlations with p < 0.1 are denoted with filled symbols.

Figure 5. Trend in the simulated (a) budburst and (b) dormancy dates for deciduous forests in the U.S. during 1982-2012. Simulations are performed with the spring model S9 and autumn model A4. The results are shown only for the grid squares where the fraction of deciduous forest is larger than 3%. Significant trends (p<0.05) are denoted with dots.

Figure 6. The (a) difference and (b) its relative change in the growth length for U.S. deciduous forests between 2000s and 1980s. Significant changes (p<0.05) are denoted with dots.

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Deleted: Trend of surface air temperature for (a, b) January, (c, d) April, and (e, f) September over deciduous forest during 1982-2012. The temperature data are from (a, c, e) MERRA reanalyses and (b, d, f) USHCN Network. Significant trends (p<0.05) are denoted with dots (a, c, e) or filled circles (b, d, f). The trends for 2000-2012 are presented in Fig. S15.

Figure 7. Comparison of phenology trend over U.S. for (a) spring and (b) autumn estimated by different studies. The U.S. domain is divided into six patches to represent different geographic areas: west, north, northeast, center, east, and southeast. In each patch, different characters represent estimates from different studies over that area. A summary of all studies used for comparison is listed in Table 1. The color of a character indicate the sign of a trend as follows: red is positive, blue is negative, and black is zero or insignificant. A patch is hatched with the same color as the dominant trend if it is non-zero.

Figure §. Interannual variations of phenological dates and their responses to temperature changes during 1992-2011 for each DBF species at Harvard Forest. The year-to-year (a) budburst and (b) dormancy onset dates are presented for species with observations available for at least 20 years. Values for red oak (*Quercus Rubra*, in red), red maple (*Acer Rubrum*, in green), and the ensemble average (in blue) based on basal area are highlighted in bold. The differences of species-specific dates relative to the ensembles are presented in (c) for budburst and (d) for dormancy onset. Temperature sensitivity of (e) budburst is calculated as the regressions between year-to-year budburst dates and March-April temperature. Similarly, regressions between dormancy onset dates and September temperature is calculated as the temperature sensitivity of (f) autumn phenology. For the middle and bottom panels, positive values are marked as red while negative ones are in blue. Significant (p < 0.05) temperature sensitivity in bottom panel is denoted with filled bar. Full names of species abbreviations are listed in Table S1, except for alternated-leaved dogwood (*Cornus Alterniflora* short as COAL) and Hawthorne (*Crataegus Sp* short as CRSP).

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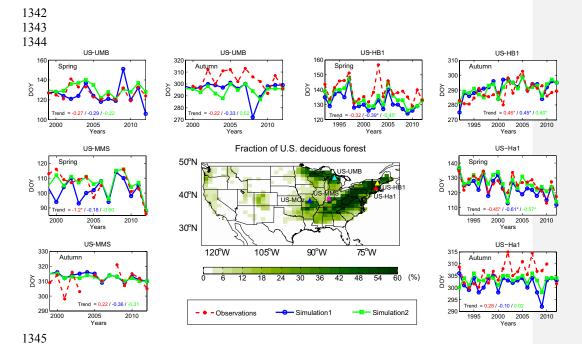


Fig. 1 Simulation of spring and autumn phenology at four U.S. deciduous broadleaf forest (DBF) sites. The map shows the fraction of U.S. DBF derived from the Advanced Very High Resolution Radiometer (AVHRR). The area with >3% coverage is the domain for this study. Five triangles indicate the locations of sites whose long-term measurements of meteorology and phenology are used for the calibration and/or validation of the model: Harvard Forest (US-Ha1), Hubbard Brook Forest (US-HB1), Morgan-Monroe State Forest (US-MMS), University of Michigan Biological Station Forest (US-UMB), and Missouri Ozark Forest (US-MOz). Phenological dates are recorded at US-Ha1 and US-HB1 during 1992-2012. Measurements of leaf area index (LAI) and photos are used to derive phenology at US-UMB and US-MMS for 1999-2012. Derived phenological dates at US-MOz are used for model calibration but not validation and are not shown here. At each site, two simulations are performed with the spring model S9 and autumn model A4 (refer to Figure 2), driven by temperatures from either the in situ measurements (blue) or the Modern Era Retrospective-Analysis (MERRA) reanalysis (green). Trend of each time series (units: day yr⁻¹) is shown with colors indicating results from observations (red) and simulations (blue or green). Significant trends (p < 0.05) are marked with asterisks.

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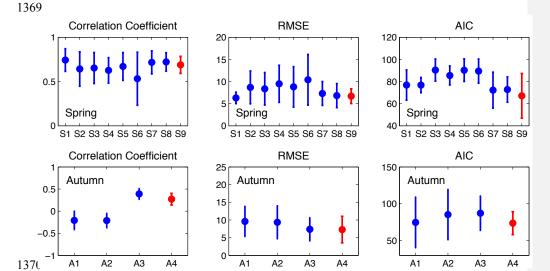


Fig. 2 Comparison of model performance in the prediction of phenological dates at four U.S. DBF sites among (top) nine spring phenology models and (bottom) four autumn phenology models. The statistical metrics are correlation coefficient, root-mean-square error (RMSE), and the Akaike Information Criterion (AIC). Each point represents the mean values of the statistical metrics at four sites for one model. The error bar represents the range of the metrics. Each model uses the optimized parameters as summarized in Table 5 for the prediction. The red ones are the models used for the continental predictions. Detailed predictions at each site are shown in Figs. S4-S11. The values of correlation coefficients, RMSE, and AIC are summarized in Table S5.

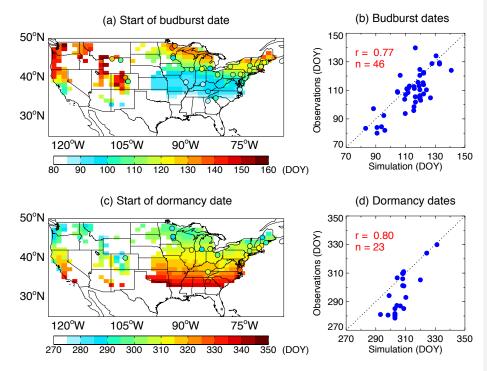


Fig. 3 Comparison of the simulated (a, b) budburst and (c, d) dormancy dates with *in situ* observations (colored circles) from the USA National Phenology Network for 2011-2012. Simulations are performed with the spring model S9 and autumn model A4. The coverage of colored patches in (a) and (c) differs from that in Figure 1 because values at and beyond the low end of color scales have been shown in white. The number of the sites and the correlation coefficients are shown in the scatter plots. The number of sites shown in the plot is much fewer than the total of 588 because only a small portion of the sites has continuous records for both years and a stringent screening process is applied to derive phenological dates (see Supplement). The separate evaluations in 2011 and 2012 are shown in Figs. S12-S13.

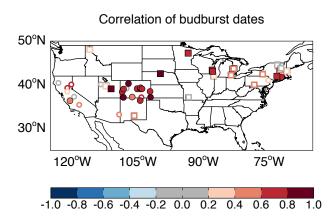
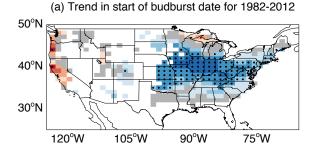


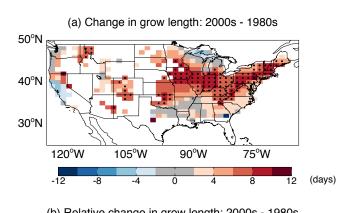
Fig. 4 Correlations (circles) between the predicted budburst dates and observed first-bloom dates from the North American Lilac Network (circle) and first-leaf dates from the USA National Phenology Network (squares). Simulations are performed with the spring model S9. The correlation coefficients are calculated for individual trees with at least 6 years of observations during 1982-2012. Correlations with p < 0.1 are denoted with filled symbols.





(b) Trend in start of dormancy date for 1982-2012 50°N 40°N 120°W 105°W 90°W 75°W -0.6 -0.4 -0.2 0.0 0.2 0.4 0.6 (day/yr)

Fig. 5 Trend in the simulated (a) budburst and (b) dormancy dates for deciduous forests in the U.S. during 1982-2012. Simulations are performed with the spring model S9 and autumn model A4. The results are shown only for the grid squares where the fraction of deciduous forest is larger than 3%. Significant trends (p<0.05) are denoted with dots.



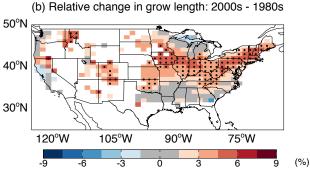
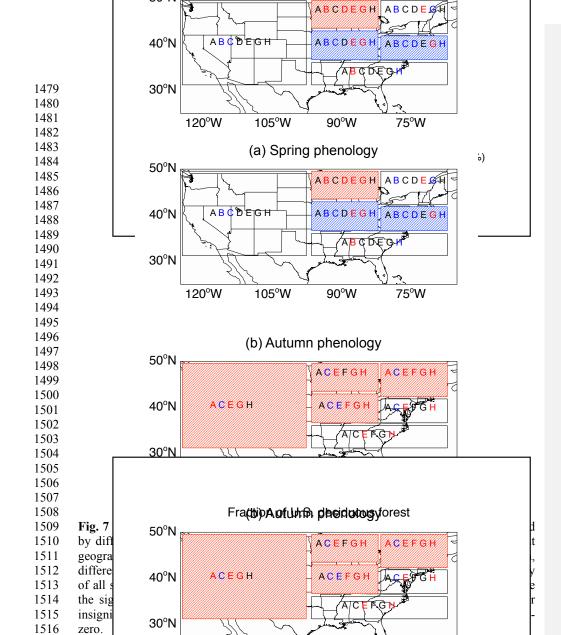


Fig. 6 The (a) difference and (b) its relative change in the growth length for U.S. deciduous forests between 2000s and 1980s. Significant changes (p<0.05) are denoted with dots.



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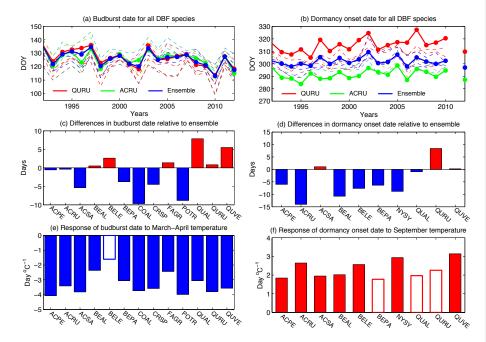


Fig. 8 Interannual variations of phenological dates and their responses to temperature changes during 1992-2011 for each DBF species at Harvard Forest. The year-to-year (a) budburst and (b) dormancy onset dates are presented for species with observations available for at least 20 years. Values for red oak (*Quercus Rubra*, in red), red maple (*Acer Rubrum*, in green), and the ensemble average (in blue) based on basal area are highlighted in bold. The differences of species-specific dates relative to the ensembles are presented in (c) for budburst and (d) for dormancy onset. Temperature sensitivity of (e) budburst is calculated as the regressions between year-to-year budburst dates and March-April temperature. Similarly, regressions between dormancy onset dates and September temperature is calculated as the temperature sensitivity of (f) autumn phenology. For the middle and bottom panels, positive values are marked as red while negative ones are in blue. Significant (p < 0.05) temperature sensitivity in bottom panel is denoted with filled bar. Full names of species abbreviations are listed in Table S1, except for alternated-leaved dogwood (*Cornus Alterniflora* short as COAL) and Hawthorne (*Crataegus Sp* short as CRSP).