FOREST ECOLOGY

Increased growing-season productivity drives earlier autumn leaf senescence in temperate trees

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Changes in the growing-season lengths of temperate trees greatly affect biotic interactions and global carbon balance. Yet future growing-season trajectories remain highly uncertain because the environmental drivers of autumn leaf senescence are poorly understood. Using experiments and long-term observations, we show that increases in spring and summer productivity due to elevated carbon dioxide, temperature, or light levels drive earlier senescence. Accounting for this effect improved the accuracy of senescence predictions by 27 to 42% and reversed future predictions from a previously expected 2- to 3-week delay over the rest of the century to an advance of 3 to 6 days. These findings demonstrate the critical role of sink limitation in governing the end of seasonal activity and reveal important constraints on future growing-season lengths and carbon uptake of trees.

The phenological cycles of trees exert a strong control on biological interactions (1, 2), the global carbon cycle, surface albedo, and the climate system (3). Warming trends over recent decades have led to extended growing seasons in temperate forests (4). As a result, primary productivity of temperate forests is expected to increase, with each day advance in spring leaf-out translating to an increase in net carbon uptake of 45 kg carbon per hectare forest and each day delay in autumn senescence translating to an increase of 98 kg ha^{-1} (5). Accurate projections of growing-season duration are, therefore, essential to forecast future changes in forest carbon balance (6). Yet, whereas spring leaf emergence has received much scientific attention (7–9), autumn phenology is relatively understudied (10), and existing models exhibit high uncertainty due to our limited understanding of the underlying environmental triggers (11). Understanding the physiological mechanisms governing the timing of autumn leaf senescence is critical if we are going to constrain the uncertainty in future projections of temperate tree phenology and productivity.

It has traditionally been accepted that autumn temperature and day length are the main determinants of autumn phenology, leading to the assumption that warming temperatures will delay autumn leaf senescence in the future (12). However, a growing body of evidence suggests that autumn delays will be counteracted by lagged effects of changes in spring and summer temperatures (11, 13). For instance, earlier leaf unfolding in spring has been found to advance autumn leaf senescence (14–16). A likely explanation is sink limitation of photosynthesis, mediated through interac-tions between photosynthate supply, phytohor-mones, and nutrient supply (17–19). Increased photosynthetic activity causes plants to pro-gress through their seasonal cycle more rapidly, ultimately resulting in earlier leaf senescence (17). This role of photosynthesis in governing the timing of leaf senescence through source-sink feedbacks has long been established in herbaceous plants (20, 21) but has never been tested in trees. Alternatively, direct constraints on leaf life span (22), increased drought stress (23), and extended herbivory (24) might ex-plain lagged effects of spring leaf-out and summer climate on tree autumn phenology. Because the underlying mechanisms remain unclear, phenological lagged effects are not, or only partially, accounted for in current autumn phenology models (11, 12). Testing the relative importance and magnitude of these effects and evaluating the implications for future autumn trajectories require quantitative, empirical evi-dence about these effects from a combination of controlled experiments and long-term in situ observations on mature trees exposed to real-world environmental changes.

In this work, we used climate-manipulation experiments and direct leaf phenology obser-vations on dominant Central European tree species to test the degree to which the timing of autumn senescence is determined by preced-ing seasonal productivity. These effects were evaluated relative to the individual effects of spring leaf-out, water availability, vapor pressure deficit, CO_2 concentration ([CO_2]), and summer and autumn temperatures. We hypothesized that, if growing-season duration is constrained by trees' carbon-sink capacity (17), then increased source strength (carbon uptake in spring and summer) should drive earlier leaf senescence in a warming, CO_2-enriched world (18). We further expected that spring leaf-out, [CO_2], summer temperature, and water availability will indi-rectly affect the timing of leaf senescence by modulating growing-season carbon uptake.

Our in situ analysis is underpinned by a database of phenological observations of spring leaf-out and autumn leaf-senescence dates collected from the Pan European Phenology Project (25). After initial filtering, we obtained 434,226 phenological observations of six decid-uous tree species at 3855 sites across Central Europe, resulting in a total of 14,626 individual time series (lasting 15 to 65 years) during the period 1948 to 2015 (table S1) (26). We then tested the relative effects of six parameters, i.e., leaf-out time, photosynthesis, vapor pressure deficit, summer and autumn temperature, and precipitation, on autumn senescence dates. To further support the results obtained from the observational data, we performed a set of con-trolled experiments, designed to modify plant carbon uptake. Finally, we developed an au-tumn phenology model that explicitly accounts for both seasonal carbon uptake and autumn environmental cues by incorporating mech-anistic representations of these drivers. To represent seasonal productivity in our analyses, we used direct photosynthesis measurements for our experiments and a parameterized pho-tosynthesis model commonly used in dynam-ic global vegetation models (27) as well as a simpler growing season index (28) for the in situ analysis (26). We compared model performance with existing autumn phenology models and used climate and spring leaf-out forecasts to project future changes in autumn senescence under a business-as-usual climate scenario. Ultimately, this combination of long-term observations, experiments, and modeling approaches enables us to evaluate the mech-anisms governing the timing of autumn leaf senescence and to improve our confidence in future forecasts of leaf phenology, carbon cycling, and climate.

Analysis of long-term observations

The long-term observations showed that across all study species, years with elevated spring-summer productivity [estimated from a param-eterized photosynthesis model (27) including information on atmospheric CO_2 levels (29), temperature, irradiance, and soil moisture] were associated with earlier autumn senes-cence (mean time series-level $R^2 \pm$ SD = 0.34 ± 0.18 Fig. 1A); after controlling for autumn temperature, each 10% increase in seasonal photosynthetic activity (relative to the mean time seasonal activity of each time series) translated to senescence 8 days (8.1 ± 3.9) earlier, on average. Across all observations [see Fig. S1 for univariate correlations among all potential drivers of leaf senescence (30, 31)] and within time series (Fig. 1 and Fig. S2), growing-season photosynthesis had the great-est effect on autumn senescence dates, relative to other physiological or environmental cues. Specifically, whereas growing-season photo-synthesis explained, on average, 34% of the

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Fig. 1. The effects of seasonal photosynthesis, autumn and summer temperatures, summer precipitation, growing-season vapor pressure deficit (VPD$_{GS}$), and spring phenology on autumn senescence dates. (**A**) Univariate effect of seasonal photosynthesis (cA$_{tot}$) on the timing of autumn leaf senescence across 14,626 analyzed time series in six species. To visualize the average trend across time series, mixed-effects models were applied, including each time series (species-site combination) as a random effect. The R^2 represents the mean coefficient of determination across all time series. (**B**) Mean partial correlation coefficients (±2 standard errors) between each parameter and senescence dates across all time series from multiple linear regression. (**C**) Causality networks for the association among environmental parameters and autumn phenology as inferred from structural equation models (SEMs) excluding (climate-driven model) or including (photosynthesis-driven model) information on seasonal photosynthesis. R^2 values represent the adjusted coefficients of variation correcting for the number of predictors. Standardized correlation coefficients between variables are shown next to lines, blue boxes indicate a negative net effect of the variable on autumn senescence, and red boxes indicate a positive effect. See table S2 for details on SEM analysis and section 1.5 in (26) for detailed variable description. To standardize among time series, variables were computed as anomalies within each time series.
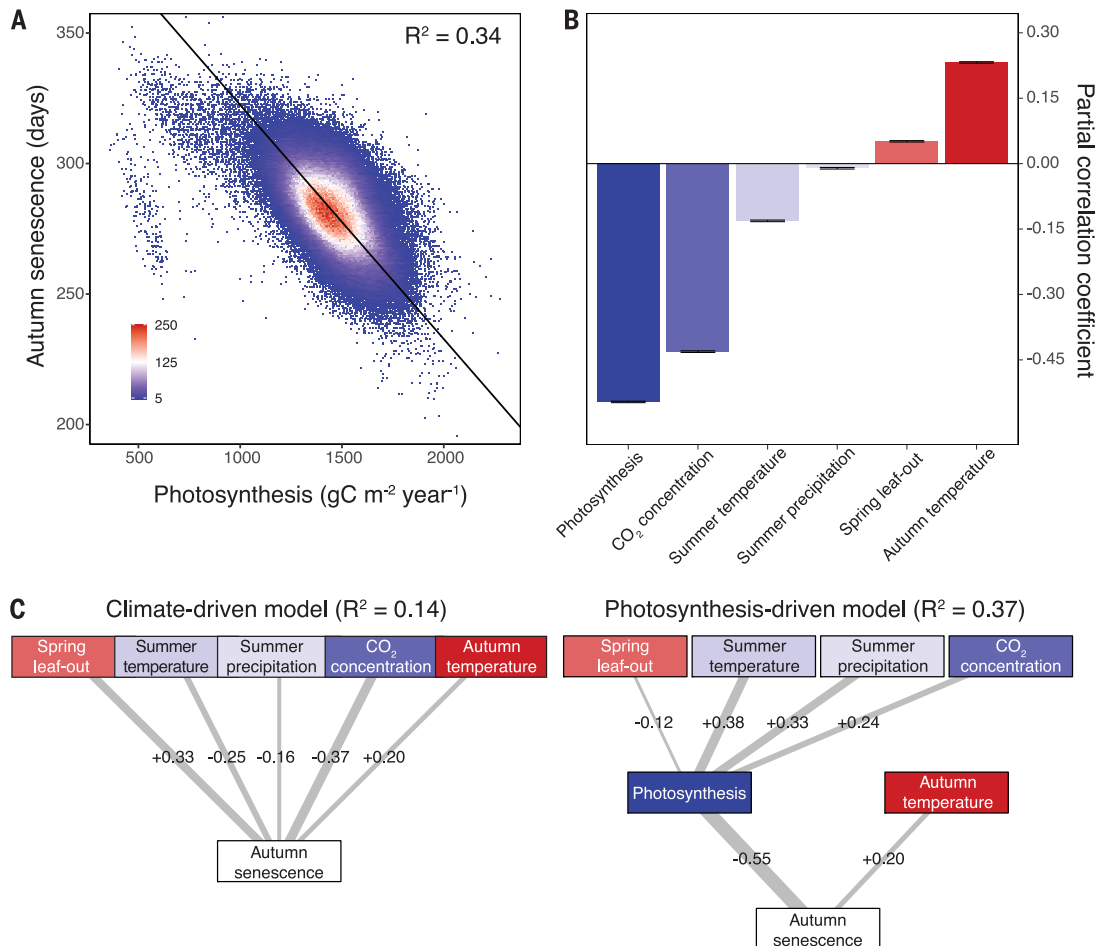
inter-annual variation in senescence dates within time series, autumn temperatures, summer temperatures, growing-season vapor pressure deficit, and precipitation individually explained 10, 7, 7, and 4% of the variation, respectively. To explore the mechanistic links between growing-season photosynthesis, spring leaf-out, climate drivers, and autumn senescence dates, we applied a structural equation model, including or excluding growing-season photosynthesis as a predictor (Fig. 1C and table S2). These analyses show the importance of photosynthesis by revealing that a combination of environmental variables alone cannot explain observed autumn senescence dates (R^2 including or excluding growing-season photosynthesis = 0.55 and 0.13, respectively). This model suggests that spring phenology, growing-season vapor pressure deficit, summer temperature, and precipitation affect the timing of leaf senescence indirectly, by modifying seasonal photosynthesis, whereas autumn temperature directly affects autumn phenology.

Experimental tests of the productivity–autumn phenology relationship

To isolate the mechanisms driving the correlations between growing-season productivity and autumn phenology, we ran a series of manipulative experiments. First, we shaded whole plants (shade treatment) or only half of a plant (half-shade treatment) of *Fagus sylvatica* and *Spiraea japonica* during the growing season and compared them, respectively, with Sun-exposed plants or the Sun-exposed halves (see materials and methods, Fig. 2A, and fig. S3 for detailed setup). Although measured leaf-level growing-season photosynthesis was strongly reduced in both shaded treatments (fig. S4A), plant-level photosynthesis was constant between the Sun-exposed and shaded halves of plants (Fig. 2B). In agreement with the sink-limitation hypothesis, senescence in fully shaded plants was delayed by, on average, 13 ± 7 and 8 ± 5 days (mean ± 95% CIs) relative to Sun-exposed individuals for *Fagus* and *Spiraea*,

respectively, whereas no significant difference in senescence dates between the shaded and Sun-exposed halves of plants could be observed (Fig. 2C). This suggests that leaf-level photosynthesis (source activity) does not directly affect the timing of leaf senescence, and, instead, autumn senescence appears to be triggered by a systemic response mediated by the interaction between plant-level sink strength and photosynthetic activity.

In a second experiment, we tested the effects of CO_2 fertilization and increased temperatures on autumn senescence dates by studying variations in spring-to-summer photosynthesis and autumn senescence dates of *Betula pendula* between three controlled climate chamber treatments (elevated temperature, elevated [CO_2], both elevated) and an ambient control. The results match our predictions based on plant sink limitation, showing that an increase in measured spring-to-summer photosynthesis of 5, 35, and 42% under elevated temperatures, elevated [CO_2], or elevated temperatures and
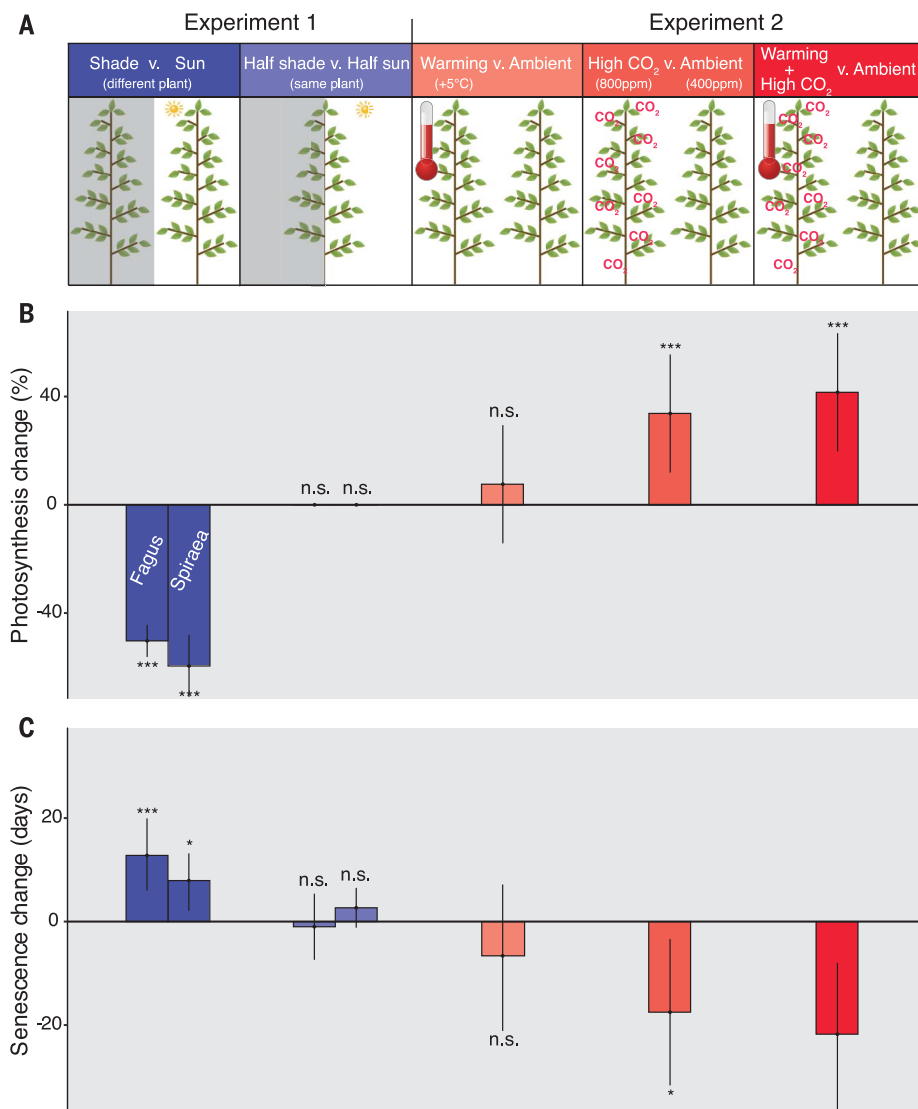
Fig. 2. Experimental tests of the effects of plant-level photosynthesis on autumn senescence dates. (**A**) Experimental setup. In experiment 1, we shaded whole plants (shade treatment) or only half of each plant (half-shade treatment) of *F. sylvatica* and *S. japonica* during the 2017 growing season [left and right blue bars in (B) and (C), respectively]. These treatments were compared with unshaded plants for the shade treatment or to the unshaded halves for the half-shade treatment. In experiment 2, *B. pendula* individuals kept in climate chambers were exposed to elevated temperatures (+5 °C), elevated [CO_2] [800 parts per million (ppm)], or a combination of elevated temperatures and [CO_2] and compared with an ambient control (400 ppm [CO_2]). v., versus. (**B**) Relative changes in plant-level spring and summer photosynthesis compared with the controls (mean ± 95% CIs). Whereas leaf-level photosynthesis of the shaded halves of plants was reduced relative to the Sun-exposed halves (see fig. S4A), there was no difference in plant-level photosynthesis between the shaded and Sun-exposed halves of plants. Note that photosynthesis reflects electron transport rates in experiment 1 and net daytime CO_2 uptake in experiment 2 (*26*). (**C**) Changes (in days) in autumn senescence dates relative to the controls. n.s., nonsignificant, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

[CO_2], respectively, translated to leaf senescence 7, 17, and 22 days earlier (Fig. 2 and fig. S5). Ultimately, across all experimental manipulations, treatments that enhanced growing-season photosynthesis caused proportionally similar advances in autumn senescence, whereas treatments that restricted growing-season photosynthesis delayed leaf senescence. Both experiments lend support for the effects of growing-season productivity and sink limitation on the timing of autumn senescence dates in temperate woody plants.

The photosynthesis-influenced autumn phenology model

To represent the observed effects of growing-season productivity on the timing of autumn senescence in phenological model forecasts, we used the in situ observational data (*25*) to develop a set of photosynthesis-influenced autumn phenology (PIA) models and tested their performance against existing models from the literature (see table S3 for a summary of

autumn phenology models). To account for the linear effect of seasonal photosynthesis on autumn senescence dates (Fig. 1A), our PIA models predict the critical cold-degree-day threshold in autumn as a linear function of seasonal photosynthesis (*26*) (Eqs. 53 to 55), assuming that increased growing-season productivity decreases the amount of autumn cooling required to induce leaf senescence. Previous models solely account for autumn temperature and day length (*12*) (first-generation models) and can additionally represent the potential influence of changing spring leaf-out (*15*), growing-season temperature, and precipitation (*11*) (second-generation models). Across all species, we found that our PIA models had higher power to predict observed leaf-senescence anomalies than did first- and second-generation models (Fig. 3 and table S4). Across the entire study period, the coefficient of determination (R^2 ± 2 standard errors) for the PIA models was 0.78 ± 0.01, relative to 0.62 ± 0.01 and 0.21 ± 0.01 for

the best-performing second-generation and first-generation model, respectively (see Fig. 3, A and B, and fig. S6 for a comparison of model fit across time). Model error in the PIA models was reduced by more than one-third compared with previous models [mean root mean square error (RMSE) ± 2 standard errors = 10.87 ± 0.05 and 6.41 ± 0.03 for the best-performing second-generation (temperature- and precipitation-influenced Delpierre model, [TPDM]) and PIA model, respectively; Fig. 3C]. The slope components of observed versus predicted autumn anomalies were close to 1 for the PIA models, indicating that the models are unbiased, whereas the slopes strongly differed from 1 for the previous models (Fig. 3D). The best-performing PIA model was our photosynthesis model accounting for water stress (PIA+), and the simpler growing season–index model (PIA$_{GSI}$) performed only marginally worse (Fig. 3). K-fold cross-validation at the time series level confirmed the stability of our predictions (Fig. 3C and table S4). The high
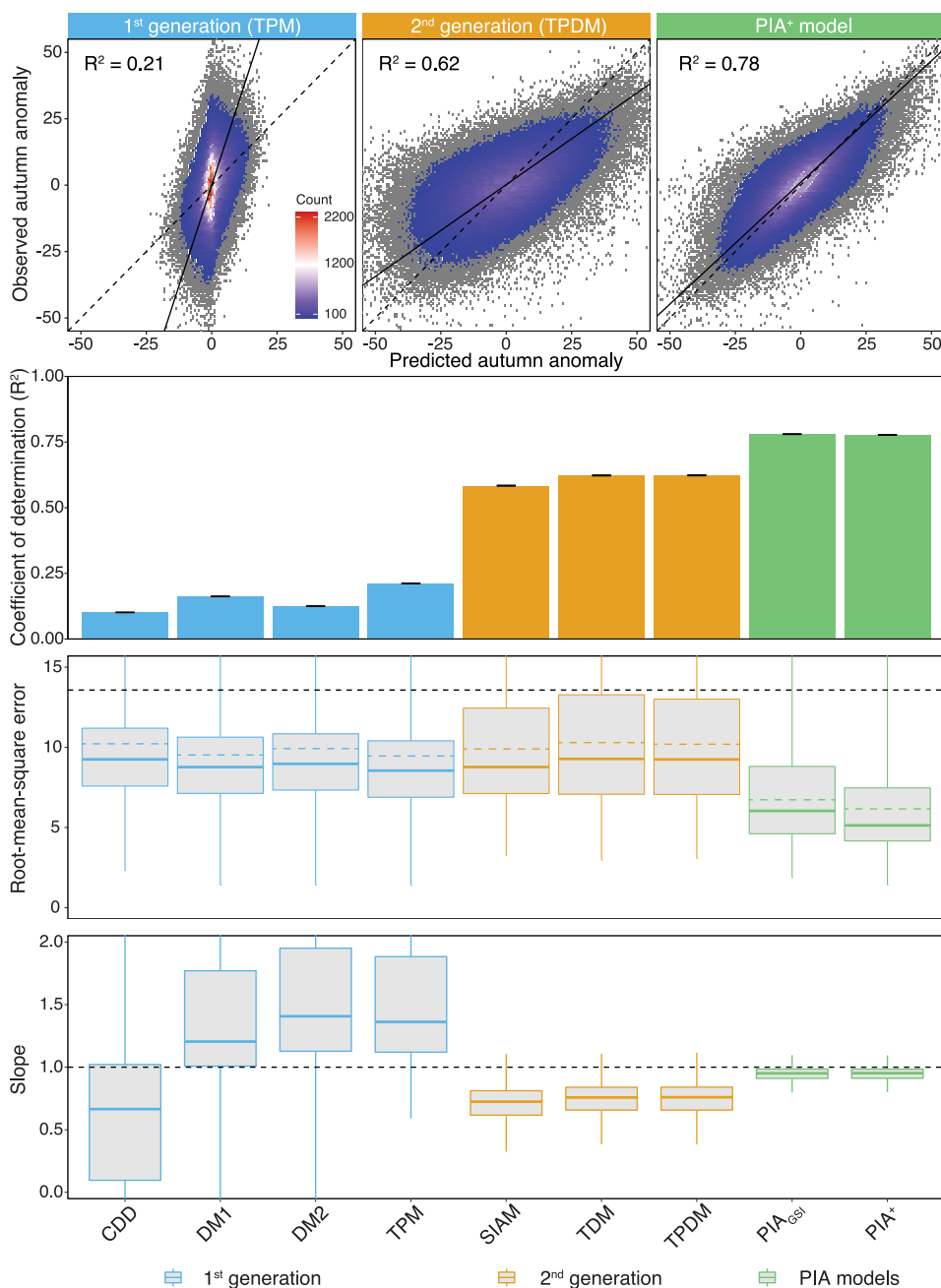
Fig. 3. Model comparison and validation of the PIA model. (**A**) Observed versus predicted autumn senescence dates of the PIA models and the best-performing first-generation and second-generation models. Solid lines show linear regression fit; dashed lines show the 1:1 line. To standardize among time series, observed and predicted senescence dates are shown as anomalies, i.e., as deviation from the mean observed senescence date of each time series. The R^2 values represent the mean coefficient of determination across all time series. (**B** to **D**) Comparison of the nine models tested in this study. (B) Mean coefficient of determination (R^2) ± 2 standard errors of observed versus predicted senescence dates across the 14,626 time series. (C) RMSEs within each time series. The colored dashed lines show the median RMSEs from fivefold cross-validation within time series; the black dashed line shows the median RMSE expected under a null model in which senescence dates do not differ among years. (D) Slope estimates of observed versus predicted senescence dates. CDD, Cold-degree-day model; DM, Delpierre model; SIAM, Spring-influenced autumn phenology model; TDM, Temperature-influenced Delpierre model; TPM, Low Temperature and Photoperiod Multiplicative model; TPDM, Temperature- and Precipitation-influenced Delpierre model.

predictive power and accuracy of our autumn phenology models provide further evidence for the important role of spring and summer plant activity in regulating the timing of autumn phenology.

Future projections of autumn phenology

Accounting for the effect of seasonal photosynthesis on autumn senescence dates in forests will be integral to improving the performance of global biogeochemical models. Current vegetation models, such as the Lund-Potsdam-Jena general ecosystem simulator (LPJ-GUESS) (32), assume a unidirectional relationship between carbon uptake and growing-season length. The assumption is that growing-season length, which itself is modeled on the basis of temperature parameters in summergreen vegetation types (33), determines seasonal carbon capture, not vice versa. As a result of this assumption, vegetation models predict increases in seasonal tree productivity due to ever-longer growing seasons under future warming conditions (6). By contrast, the direct control of the growing-season end by the extent of preceding carbon capture (Figs. 1 and 2) predicts that ever-earlier start dates of photosynthetic activity (4, 5) and increased activity during the season (34) will drive earlier autumn senescence in the future, placing a constraint on growing-season lengths and the seasonal carbon-capture potential of temperate trees.

We further explored these implications of changes in seasonal productivity on future projections of autumn phenology (Fig. 4, A and B) and growing-season length (Fig. 4. C and D) by running the two best-performing first-generation, second-generation, and PIA models based on climate projections from a business-as-usual emissions scenario (representative concentration pathway [RCP] 8.5) over the rest of the century (see figs. S7 and S8 for species-level results). On average, across all time series (species–site combinations), the first-generation models projected senescence delays ranging between 17 and 19 days by the end of the 21st century (see Fig. 4B and fig. S8 for species-level results), which results from
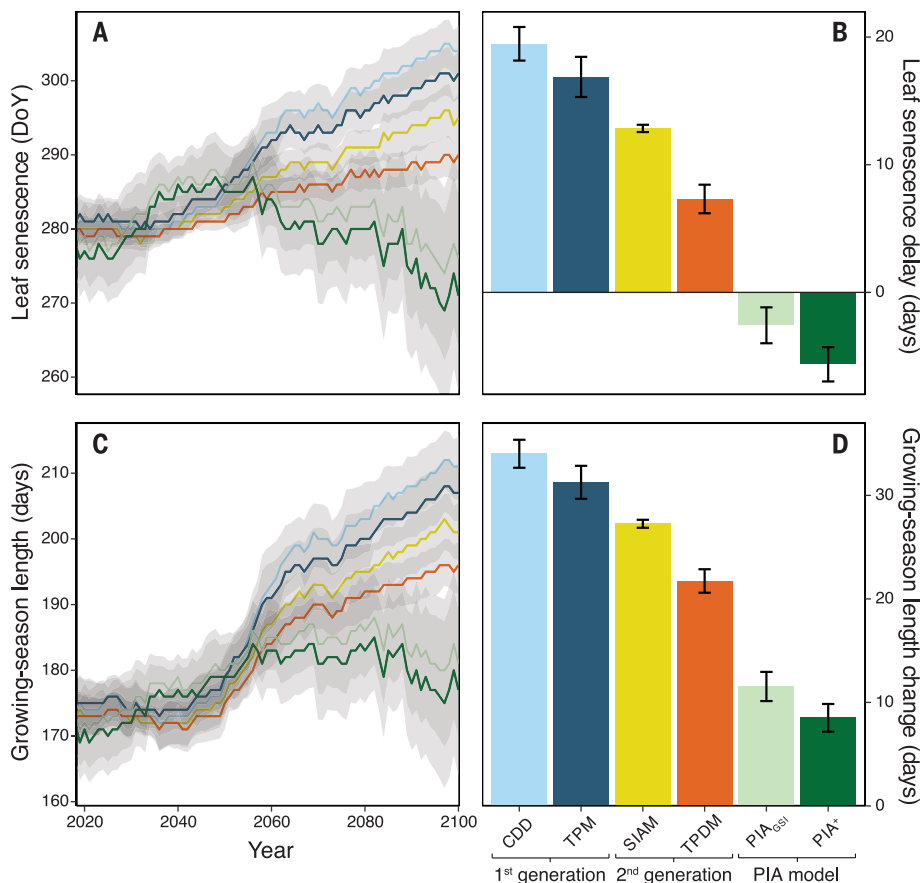
Fig. 4. Future projections of autumn senescence dates and growing-season lengths in Central European deciduous trees. (**A**) Senescence projections (15-year moving averages for six species) under the RCP 8.5 ("business-as-usual") climate scenario, based on the first-generation (CDD and TPM), second-generation (SIAM and TPDM), and PIA models. The gray area indicates 1 SD on either side of the mean. DoY, day of year. (**B**) Estimated delays in leaf senescence by the end of the 21st century (2080 to 2100) compared with the average senescence dates between 1990 and 2010. (**C** and **D**) Same as (A) and (B) but showing overall growing-season length instead of autumn senescence dates. Future leaf-out date predictions to calculate growing-season lengths are based on the M1 spring phenology model.

the large importance of autumn temperatures in these models. Second-generation models projected less pronounced senescence delays (7 to 13 days) because the earlier spring leaf-out and elevated summer temperatures constrain the response of leaf senescence to future autumn warming. In contrast to the delayed senescence predicted by both sets of models, our PIA models project a slight advance of senescence, suggesting that, if growing-season photosynthesis continues to increase, leaves may senesce 3 to 6 days earlier in the year by the end of the century. Our models, therefore, predict that the effect of autumn temperature predominant in first- and second-generation models will be outweighed by increasing spring and summer productivity in the future, reversing expectations of future changes in autumn phenology. With a predicted increase in overall growing-season length by 31 to 34 days at the end of the 21st century in first-

generation models, by 22 to 27 days in second-generation models, and by only 8 to 11 days in our PIA models (Fig. 4D), these new predictions lower our expectations of the extent to which longer growing seasons will increase seasonal carbon uptake in forests.

Discussion

The most likely explanation for the negative relationship between seasonal productivity and autumn senescence dates is the control of photosynthesis by sink activity (*17*). The seasonal carbon-sink capacity of plants is limited by nutrient (in particular nitrogen) supply (*17, 35*) and developmental and translocation constraints, such as tissue maturation and phloem loading (*36, 37*). In sink-limited plants, carbon uptake during the growing season should, therefore, act as a self-regulatory mechanism constraining the length of the productive season. By affecting carbon up-

take, preceding phenological stages, such as spring leaf-out, should be indirectly linked to autumn phenology (*14–16, 38*). These predictions are met in both our experiments and the in situ analyses (Figs. 1C and 2). The effect of growing-season plant productivity on autumn phenology thus offers a mechanistic explanation for how increased carbon capture in response to elevated atmospheric CO_2 is likely to be constrained in sink-limited ecosystems (*39*).

Molecular evidence for sink limitation comes from studies on herbaceous plants that highlight an important effect of source-sink regulatory networks on autumn leaf senescence (*40–42*). Carbon saturation due to a critical concentration of sugar in the sink organs has been shown to shift the metabolism of the plant to nutrient remobilization and induce leaf senescence through photosynthetic feedback inhibition (*21, 41*). We found little evidence to support the alternative hypothesis that lagged effects on autumn phenology are explained by constraints on leaf longevity or water stress (*15, 23*), as changes in leaf-level photosynthesis did not directly affect autumn senescence (see half-shade treatment in Fig. 2) and low water availability in summer tended to delay, not hasten, autumn senescence (Fig. 1B). Spring leaf-out timing per se was a weaker predictor of autumn phenology than was growing-season productivity (Fig. 1B and fig. S2).

Our results now offer a framework for unifying previous results that earlier spring leaf emergence and warmer summers advance the timing of autumn phenology, whereas drier leafy seasons delay it (*14, 30, 31*) (Fig. 1, B and C, and fig. S2): Earlier leaf emergence and warmer summer periods increase growing-season photosynthesis and should thus accelerate sink saturation and leaf senescence (Fig. 1, B and C). By contrast, repeated seasonal droughts impair sugar transport from the leaf to the sink, thus delaying the senescence process (*43*). These effects are explicitly captured by our photosynthesis models because we use leaf-out dates to determine the start of seasonal photosynthesis and include a drought-stress index in our photosynthesis calculation.

Our analysis of the environmental and internal controls of autumn phenology suggests that seasonal productivity is an important driver of leaf senescence in temperate deciduous trees. Increased growing-season productivity led to earlier leaf senescence in our climate-manipulation experiments and across our 434,226 tree observations over the past 6 decades. Our autumn senescence model representing this internal control mechanism outperformed previous models in the literature and reversed expectations of future changes in autumn phenology: Although autumn warming is likely to increase over the rest of the

century, our model forecasts that there might be slight advances, not delays, in autumn senescence dates. This can be explained by sink limitation of plant growth, predicting that carbon uptake during the growing season imposes strong constraints on the length of the productive season through feedbacks between source and sink organs in plants. These results highlight physiological constraints on growing-season lengths and plant productivity in a warming, CO_2-enriched world, which has direct implications for future carbon-cycle and climate projections. An important avenue of research is the implementation of such growing-season length constraints in Earth system and vegetation models, which currently do not consider the role of source-sink feedbacks when predicting the seasonal CO_2 uptake of plants (44). Furthermore, given that ecosystems with high nutrient availability and minimal carbon-sink limitation, such as regions dominated by nitrogen-fixing trees, are not expected to show the observed negative relationship between seasonal productivity and senescence dates (45), a major research challenge will be to generate a thorough spatial understanding of the extent of sink limitation to forecast plant phenology and forest productivity over space and time.

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SUPPLEMENTARY MATERIALS

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Materials and Methods
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Science

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Limits to the growing season

The length of the growing season in temperate forests has been increasing under recent climate change because of earlier leaf emergence and later leaf senescence. However, Zani *et al.* show that this trend might be reversed as increasing photosynthetic productivity begins to drive earlier autumn leaf senescence (see the Perspective by Rollinson). Using a combination of experimental, observational, and modeling studies based on European forest trees, the researchers conclude that leaf senescence will advance by 3 to 6 days by the end of the 21st century rather than lengthening by 1 to 3 weeks as current phenological models have predicted. In turn, this predicted phenological pattern will limit the capacity of temperate forests to mitigate climate change through carbon uptake.

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