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No evidence for a negative effect of growing season photosynthesis on leaf senescence timing

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Abstract

The length of the growing season has a large influence on the carbon, water and energy fluxes of global terrestrial ecosystems. While there has been mounting evidence of an advanced start of the growing season mostly due to elevated spring air temperatures, the mechanisms that control the end of the growing season (EOS) in most ecosystems remain relatively less well understood. Recently, a strong lagged control of EOS by growing season photosynthesis has been proposed, suggesting that more productive growing seasons lead to an earlier EOS. However, this relationship has not been extensively tested with *in-situ* observations across a variety of ecosystems. Here, we use observations from 40 eddy-covariance flux tower sites in temperate and boreal ecosystems in the northern hemisphere with more than 10 years of observations (594 site-years), ground observations of phenology, satellite observations from the Moderate Resolution Imaging Spectroradiometer (MODIS) and three leaf senescence models to test the extent of a relationship between growing season photosynthesis and end of season senescence. The results suggest that there is no significant negative relationship between growing season photosynthesis and observed leaf senescence, flux-inferred EOS estimates, or remotely sensed phenological metrics, in most ecosystems. On the contrary, while we found negative effects of summer air temperatures and autumn vapor pressure deficit on EOS, more productive growing seasons were typically related to a later, not earlier, EOS. Our results challenge recent reports of carry-over effects of photosynthesis on EOS timing, and suggest those results may not hold over a large range of ecosystems.

1. Introduction

Global terrestrial ecosystems take up around one third of human emission of CO_2 (Friedlingstein et al., 2020). With recent climate change, the seasonality of terrestrial ecosystems, a sensitive indicator of biosphere-climate interactions, has been reported to be changing (Piao et al., 2007; Seddon et al., 2016). Longer growing seasons have been associated with increased carbon uptake by many ecosystems (Keenan et al., 2014), but the dominant controls of the growing season length remain relatively poorly understood.

The start of growing season (SOS) has been found to have advanced in most ecosystems and is known to be largely controlled by air temperature in temperate and boreal ecosystems (Chmielewski & Rötzer, 2002; Song et al., 2010; Yu et al., 2013). However, modelling of the timing of the end of growing season (EOS) has been challenging, as the mechanisms that control the EOS have not been thoroughly investigated or well understood (Lang et al., 2019; Zhang et al., 2020), and many studies found a much smaller scale of EOS changes compared with the SOS changes (Jeong et al., 2011; Park et al., 2016). There are many factors that may contribute to the changes of EOS, such as the limiting factors of plant productivity of air temperature, radiation, soil moisture and VPD (Archetti et al., 2013; Körner & Basler, 2010). At the same time, other factors such as nutrient supply, sink limitation and photoperiod, as well as a potential influence of soil moisture limitation on EOS globally (Buermann et al., 2018; Liu et al., 2016; Lian et al., 2021) may also play a role in EOS changes.

Recently, it has been suggested that growing season photosynthesis may have a significant negative impact on EOS in some plants. That is to say, if the plants had a very productive growing season, they are more likely to senesce their leaves early (Zani et al., 2020). Zani et al., (2020) used observations from the European Phenology Network and controlled experiments to test the effects of growing season photosynthesis on the timing of leaf senescence and found that more productive growing seasons led to earlier leaf senescence in central European forests. They hypothesized a strong role of sink limitation in these species. However, they modelled the gross primary productivity (GPP) following the Lund-Potsdam-Jena General Ecosystem Simulator (LPJ-GUESS) model, which may introduce some uncertainties due to the model parameterization, and the study was limited to specific species in central Europe. Also, their results contradict the findings of most free-air CO_2 enrichment (FACE) experiments, in which the leaf senescence dates are typically either delayed or remained unchanged (Norby, 2021). An earlier senescence under higher GPP would have large implications for expected EOS changes under climate change, but further testing with more diverse and distributed phenology and photosynthesis observations is needed.

Typically, phenological metrics of different species are recorded by visual observations, or digital cameras at specific sites (Richardson et al., 2018a). The most successful efforts include the European phenology network and the USA National Phenology Network that provide more than 60 years of observations (van Vliet et al., 2003). In recent years, the seasonal cycles of remotely sensed observations such as vegetation indices (VIs), sun-induced fluorescence and vegetation optical depth, and flux tower observations have also been widely used to estimate key phenological metrics at landscape and larger scales (D'Odorico et al., 2015; Gonsamo et al., 2012; Joiner et al., 2014; Wu et al., 2017; Yang & Noormets, 2021; Zhang et al., 2019). These metrics provide insight into the changes of seasonal cycles of greenness and/or carbon fluxes in a diverse array of ecosystems, with

significant potentials for understanding phenology-climate interactions (Tang et al., 2016). These global and regional observations also provide a unique opportunity to test phenological hypotheses in different ecosystems, particularly when co-located eddy-covariance (Novick et al., 2018; Pastorello et al., 2020), ground and remote sensing observations can be combined.

In this study, we used flux observations from 40 eddy-covariance sites that have measurement records of more than 10 years to test the relationship between growing season photosynthesis and EOS across a variety of ecosystems. These sites represent a large subsection of main biomes in North America and Europe (8 biome types according to the International Geosphere-Biosphere Program (IGBP)) from 1992 to 2017 and have a total of 589 site-years of observations. In addition, we used long-term ground phenological records co-located with eddy-covariance measurements at a site in the northeastern US (Harvard Forest), along with phenological metrics from the MODIS global land cover dynamics product at all sites studied, and three leaf senescence models. Doing so, we aim to address the following questions:

1) Are there significant carry-over effects of growing-season photosynthesis on EOS in most sites and ecosystems?
2) What are the most important factors that contribute to EOS changes?
3) Does the introduction of growing-season photosynthesis improve model predictions of EOS?

2. Methods and materials

2.1 Flux tower measurements
We used 40 sites from the FLUXNET 2015 dataset (http://fluxnet.fluxdata.org/, (Baldocchi, 2008; Pastorello et al., 2020)) and AmeriFlux (https://ameriflux.lbl.gov/, (Novick et al., 2018; Keenan et al., 2019)) in this study (Table S1). We focused on ecosystems that had a strong seasonal cycle of photosynthesis (e.g., no tropical sites were selected). Also, we removed sites that had a double growing season (i.e., double peaks in the growing season GPP most likely due to site management and/or water stress), as indicated by the GPP time series (Fig. S1). For sites in both the FLUXNET 2015 and AmeriFlux databases, we chose the source with a longer record of observations.

For 12 out of 15 sites within AmeriFlux that do not provide gap-filled and partitioned data, we used the R package REddyProc to gap-fill and partition net ecosystem change (NEE) into GPP and ecosystem respiration (R_{Eco}) using the nighttime partitioning model (Reichstein et al., 2005, Wutzler et al., 2018). Similar results were found when using the daytime partitioning method (Fig. S2, Lasslop et al., 2010).

To determine growing season photosynthesis, we summed up the hourly or half-hourly GPP

within the period. We determined the start of the growing season as outlined in section 2.4 and used the first day that has daylength of fewer than 11.2 hours as the end date for the calculation of end of growing season photosynthesis (in order to avoid introducing spurious correlations between EOS and growing season photosynthesis, following Zani et al., 2021). Also, following the method used in Fu et al., 2017, we calculated the environmental conditions (air temperature (T_{air}), vapor pressure deficit (VPD) and global radiation (R_g)) in different seasons in the Northern Hemisphere (Summer: June, July and August; Fall: September, October and November).

2.2 Phenological records from Harvard Forest

We used observations from the Phenology of Woody Species at Harvard Forest dataset from 1991 to 2017, obtained from the Harvard Forest Data Archive (hf003-08, O'Keefe, 2019; Richardson et al., 2006). Phenological observations (spring and fall) have been recorded for more than 33 woody species around the Harvard Forest starting from 1991 (for spring phenology) and 1992 (for autumn phenology). Leaf phenology dates were recorded by looking at the percentage of the leaves that have emerged (spring) and dropped (fall). We used the dates within the dataset when 50% of leaves have emerged or dropped each year. The mean fall dates at species-level provided with the data set were used and we focused on the two dominant species within the eddy-covariance tower footprint, i.e., Red Oak and Red Maple, in the forest (Finzi et al., 2020).

2.3 MODIS global land dynamics product

We used the MODIS land cover dynamics product (MCD12Q2, (Zhang et al., 2003)) downloaded from Oak Ridge National Laboratory's Distributed Active Archive Center (with a spatial resolution of 500 m, combined from Terra and Aqua, collection 6). This dataset provides a global estimate of several phenological metrics since 2001. Technically, it identifies phenological metrics derived from the seasonal time series of MODIS-observed enhanced vegetation index (EVI). The original EVI time series was gap-filled and smoothed, and then fit to a logistic model. Detailed information of the process can be found in Zhang et al., (2003), Zhang et al., (2006) and Ganguly et al., (2010). We used the date when EVI last crossed 15% (the MCD12Q2 Dormancy date) of the segment EVI amplitude, EOS, as the leaf senescence metric. We only used the pixel on which the flux tower centered from the MCD12Q2 data set.

2.4 Determination of phenological metrics from flux measurements

To determine the phenological metrics (i.e., SOS and EOS) from flux-estimated GPP, we applied a widely used double-logistic curve fitting method (Gonsamo et al., 2012). The method has proven to work well in most sites and ecosystems (D'Odorico et al., 2015; Lu et al., 2018). To retrieve the key phenological dates, we used the half-hourly GPP estimates from the FLUXNET or AmeriFlux data sets. First, we summed up the gap-filled half-hourly GPP at the daily scale; then, we filtered out years when the data coverage was not sufficient

(fewer than 100 days of GPP estimates); finally, we fit the daily GPP time series to the following double-logistic model:

$$(1)$$

The seven free parameters (a1, a2, a3, b1, b2, d1 and d2) were determined using non-linear curve fitting. a2 – a1 and a3 – a1 represent the difference between the winter background value and the amplitude of the summer peak growing season values. d1 and d2 are the transition curvature parameters, while b1 and b2 are the midpoints in DOYs of these transitions for green-up and senescence/abscission, respectively.

This method identifies the SOS as the start of the slope of the ascending curve and EOS is identified as the end of the descending curve (the inflection point). We followed the method used in Gonsamo et al., (2012) to identify the thresholds from the logistic model (1), which estimates the SOS and EOS as:

$$(2)$$

$$(3)$$

We compared the EOS estimates from both flux tower estimated GPP and remotely sensed EVI (Fig. S3). The EOS estimated by the two methods were comparable, but mismatches can be evident in some ecosystems. Overall, we found that the flux-inferred and remotely sensed EOS metrics were significantly correlated ($p < 0.01$), and especially for deciduous broadleaf forest (DBF) and mixed forest (MF) sites, though GPP EOS had a higher dynamic range in all ecosystems. For ecosystems where the seasonality of canopy greenness is more difficult to detect (e.g., grassland, GRA), the two EOS estimates varied substantially.

In order to compare the relationship between growing season photosynthesis, leaf senescence metrics and environmental conditions, we linearly detrended all time series in order to reduce the likelihood of extraneous correlations.

2.5 Modelling of leaf senescence dates

First, to analyze the relationship between environmental factors and the timing of senescence, we developed structural equation models using the Structural Equation Models Optimization in Python (semopy) package (Igolkina & Meshcheryakov, 2020). This package provides a concise way to test the structural relationships between different variables and to build structural equation models. We used structural equation models to compare three different ways of empirically predicting the EOS using environmental conditions. In model a, we used all environmental variables (summer and autumn T_{air}, summer and autumn R_g, summer and autumn VPD) to predict the EOS directly; in model b, we used summer environmental variables (summer T_{air}, summer R_g and summer VPD) to predict the growing season photosynthesis and used predicted growing season photosynthesis with autumn environmental variables (autumn T_{air}, autumn R_g and autumn

VPD) to predict the EOS; in model c, we used growing season photosynthesis from flux observations and the autumn environmental variables (autumn Tair, autumn Rg and autumn VPD) to predict the EOS.

In addition, we compared three different process-oriented leaf senescence models by examining their performance for predicting autumn senescence dates at the Harvard forest site. The first model we assessed is the cold-degree day model that combines the use of both air temperature and photoperiod (Delpierre et al., 2009). When thresholds of air temperature (T_b) and photoperiod (P_{start}) are reached, the control of air temperature and photoperiod over autumn leaf senescence is modelled via the cumulative cold-degree days as follows:

$$(4)$$

Where the CDD(d) is the cold-degree day at day(d) with the air temperature of T(d) and photoperiod P(d). Then the CDD(d) of each day is accumulated. The modeled leaf senescence date (Y_{mod}) was set as the first day that the accumulated CDD (aCDD) reached a critical threshold as follows:

$$(5)$$

Here, Y_{crit} is a threshold to be determined. In this manuscript, we refer to this model as the CDD model.

It has also been reported that spring phenology is associated with autumn phenology, and a revised version of the CDD model has been proposed to accommodate these effects (Keenan and Richardson, 2015). In this spring phenology influenced autumn phenology model (SIAM), the threshold of Y_{crit} is set as:

$$(6)$$

Here, S_a is the spring phenology anomaly of the associated years. Also, as Zani et al., (2020) suggests, growing season photosynthesis might have an impact on the end of the growing season. We therefore also modified the model as follows to represent this hypothesis:

$$(7)$$

Here, the GPP represents the growing season canopy photosynthesis. In this manuscript, we referred to this model as the photosynthesis-influenced autumn phenology (PIA) model. To estimate the free parameters in the three different models, we used the Pymcmcstat Markov-chain Monte Carlo python package (Miles, 2019). We estimated the parameters used in the three models 100 times, and sampled parameters resulting in the 95th percentile of model performance.

To examine differences in projections of future autumn phenology change from the 3 different autumn phenology models, we estimated the delays of autumn senescence date across 5 °C of projected future temperature changes. For the SIAM model, we predicted the sensitivities of spring phenology dates to air temperature to be 3 $d^{-1} °C^{-1}$ according to the model ensemble assessed in (Migliavacca et al., 2012). For the PIA model, we predicted a 6 $gC \, yr^{-1} \, m^{-2} \, °C^{-1}$ increase of growing season photosynthesis with the increase in air temperature as this is the overall slope at Harvard Forest according to our results.

3. Results

3.1 No evidence for the carry-over effects of growing season photosynthesis on EOS

At the site level, we focused on the observations from Harvard Forest, which provide a long-term record of eddy-covariance measurements and phenological metrics of Red Oak (the most dominant species in the forest, Fig. S4). We found positive but non-significant relationships between growing season photosynthesis and EOS dates either when using ground phenological records or MODIS estimates (p > 0.05).

We then examined the relationship between growing season photosynthesis and flux-estimated EOS across different ecosystems in the eddy-covariance flux network (Fig. 1). We found a significant and positive relationship between growing season photosynthesis and EOS in evergreen needleleaf forest sites (ENF) (slope = 0.24, p = 0.02). In other ecosystems, however, we did not find significant relationships between them. In DBF, GRA, and MF sites, we found a positive yet non-significant growing season GPP – EOS relationship. When all sites were pooled together, we found a significant and positive, though weak, relationship between growing season photosynthesis and flux-estimated EOS (slope = 0.1, p = 0.01).

We also tested the relationships between growing season photosynthesis and MODIS EOS in different sites and ecosystems. Except for MF sites, where we found a negative yet non-significant relationship between growing season photosynthesis and remotely sensed EOS (slope close to 0, p = 0.97), the growing season photosynthesis-EOS relationship tends to be positive yet non-significant. Overall, we found no significant relationship between growing season photosynthesis and remotely sensed EOS (slope = 0.03, p = 0.27).

Fig. 1. The relationship between growing season gross primary productivity (GPP) and phenological end of season (EOS) metrics from eddy-covariance (EC) observations or MODIS observations at deciduous broadleaf forest (DBF), evergreen needleleaf forest (ENF), mixed forest (MF), grassland (GRA) and all sites (ALL). All the time series have been detrended and the differences introduced by different sites were set as random effects.

3.2 Control of environmental factors over EOS in different ecosystems

We examined the multi-variable relationships between environmental factors and EOS

metrics in different ecosystems. First, we performed a partial correlation analysis between different environmental variables and EOS estimates at Harvard Forest (Fig. 2). For ground observations of Red Oak, we found a positive partial correlation between growing season photosynthesis and leaf senescence metrics, while we found weaker positive relationships with MODIS remotely sensed metrics. We also found contrasting effects of global radiation (Rg), air temperature and VPD in the spring and in the autumn. Both data sets indicated that higher summer Rg, lower summer temperature and lower summer VPD were associated with a later EOS; while more autumn Rg, higher autumn air temperature and higher autumn VPD led to an earlier EOS.

Fig. 2. Partial correlations between environmental variables and end of growing season (EOS) in Harvard forest using ground phenological records (a) and the MCD12Q2 product (b). The environmental variables included here were growing season photosynthesis (Photosynthesis), summer global radiation (Rg), autumn Rg, summer air temperature (Tair), autumn Tair, summer vapor pressure deficit (VPD), and autumn VPD. All the time series have been detrended. Here, summer is defined as June, July and August while fall is defined as September, October and November.

At the cross-site scale, we found more complicated relationships between flux-estimated EOS and different environmental variables (Fig. 3). First, we did not find growing season photosynthesis to be the most important factor when it came to predicting EOS in any of the ecosystems. In all ecosystems, we found a positive contribution (partial correlation) between growing season photosynthesis and EOS (r = 0.12, 0.11, 0.03 and 0.32 for DBF, ENF, MF and GRA sites respectively). Overall, we found a positive partial correlation between growing season photosynthesis and EOS (r = 0.12). The controls of environmental factors were different in different ecosystems; and the same environmental factors exhibited different impacts in different seasons. For global radiation, for example, the autumn R_g contributed most positively to the variation of EOS expect for GRA; while the summer R_g effects were mixed in different ecosystems (marginal effects found in ENF, while positive effects were found in DBF sites and negative effects in GRA and MF sites). For air temperature, interestingly, we found that summer T_{air} contributed mostly negatively to EOS (although sometimes marginally) except for GRA sites; while the autumn T_{air} contributions were mixed in different ecosystems we tested. Finally, for VPD, we also found that summer VPD effects were mostly positive except for GRA sites, while the autumn VPD effects were all negative. Overall, when all sites were used, we found a marginal contribution of summer R_g; positive contributions of autumn R_g, autumn T_{air} and summer VPD; negative contributions of summer T_{air} and autumn VPD.

Fig. 3. Partial correlations between detrended environmental variables and flux-derived EOS in different ecosystems. The environmental variables tested include growing season

photosynthesis, summer global radiation (R_g), autumn R_g, summer air temperature (T_{air}), autumn T_{air}, summer vapor pressure deficit (VPD), and autumn VPD. All the time series have been detrended. The overall linear regression model performance (correlation) using all predictors were labeled.

3.3 The introduction of growing season photosynthesis did not improve EOS predictions

Using a structural equation model analysis, we found that the introduction of growing season photosynthesis did not improve the overall model performance when using all DBF sites (Fig. 4). We tested three different structural equation models. In the first model, we used a simple multiple linear regression model to predict EOS using only meteorological variables (R = 0.43). In the second model, we used summer environmental factors to predict growing season photosynthesis, and then used the growing season photosynthesis and autumn environmental factors to predict EOS (R = 0.34). Finally, we used flux-estimated photosynthesis along with autumn environmental factors to predict EOS (R = 0.39). We found positive coefficients of photosynthesis in the latter two models (β = 0.06 for model b and β = 0.06 for model c).

Fig. 4. Analysis of the flux-inferred end of growing season in deciduous broadleaf forest (DBF) sites with three different structural equation models (see the method section). The β coefficients determined for each predictor in the structural equation models are denoted, with significant coefficients ($p < 0.05$) denoted with a *. The end of growing season (EOS) and predictors at each site have been detrended. (a) predicts EOS using the direct influence of environmental variables; (b) predicts EOS using the direct influence of environmental variables along with the indirect influence through predicted photosynthesis, and (c) predicts EOS using the direct influence of both environmental variables and eddy-covariance inferred estimates of growing season photosynthesis.

At Harvard Forest, we also tested the performance of three different end of growing season models to predict the leaf senescence dates (Table 1). In the resulting comparison it is important to note that the number of free parameters is different in different models: the CDD model requires three free parameters while the SIAM and PIA models require four free parameters. The results showed that the performance of the three models was generally comparable. Overall, however, we found that the PIM model, which introduced the growing season photosynthesis predictor, underperformed the CDD and the SIAM model. For Red Oak, the most dominant species in the forest, all three models did a relatively worse job when predicting the leaf senescence date, though within a comparable range to previous studies for other species at the forest (Keenan and Richardson, 2015).

Table 1. The model performance in predicting leaf senescence date at Harvard Forest. Here, the CDD, SIAM and PIA model represent the cold degree days model, spring phenology

impacted autumn phenology model and the photosynthesis impacted phenology model, respectively; and the RMSE denotes the root mean square error of each model.

Model	Red Oak		Red Maple	
	Correlation	RMSE	Correlation	RMSE
CDD	0.48	4.87	0.65	2.63
SIAM	0.48	4.87	0.70	2.48
PIA	0.44	4.93	0.63	2.67

While the three models (CDD, SIAM and PIA) showed similar performance for estimating the autumn senescence date, their predictions of future autumn senescence delays diverged (Fig. 5). Using the parameterized models, we found a similar response of autumn senescence delays in both the CDD and PIA models. This was mainly due to the fact that the coefficient relating growing season photosynthesis and the threshold of autumn senescence was estimated to be small in the PIA model. In both species, we also found that the SIAM model tended to predict a smaller delay in autumn senescence dates, especially for Red Maple where the SIAM model performed the best. The divergent predictions by different models despite similar performance for long-term observations of natural variability points to the need for future studies, especially controlled experiments, to fully tease apart the controls of autumn senescence to rising temperature.

Fig. 5. Projections of future delays in autumn senescence dates with increasing air temperature, as estimated by three different models. The error bars indicate the standard deviations of the predictions within the 95th percentile of model performance from the MCMC process.

4. Discussion

4.1 The carry-over effects of "growing season photosynthesis" on EOS
In the present study, our primary objective was to use flux tower observations from 40 sites across the temperate and boreal ecosystems in the Northern Hemisphere to test the carry-over effect hypothesis, which proposed significant negative effects of growing season photosynthesis on the date of leaf senescence and the end of the growing season (Zani et al., 2020).

We did not find significant carry-over effects in the ground and remote sensing observations for Harvard Forest, nor in most of the eddy-covariance ecosystems examined. For instance, we found positive but insignificant relationships in all three ground-observed phenological records at Harvard Forest. On the contrary, we found that in most sites, a more productive growing season either led to a delayed EOS or contributed little to the changes of EOS.

In addition, we also tested the possible improvement of model performance by introducing the use of growing season photosynthesis. We found that the growing season photosynthesis influenced models did not outperform the previous empirical models (structural equation model) or process-based models (CDD and SIAM models). And with future warming, our results show that model choice can lead to considerable differences in the future phenological shifts. This is true even in the absence of considering a CO_2 effect on photosynthesis, which would likely lead to more divergent predictions between the CDD and PIA models. That said, our results indicate small, and in most cases positive, coefficients between growing season GPP and Y_{crit}, which suggests that incorporating a CO_2 effect on photosynthesis is unlikely to greatly influence PIA model projections for our studied sites.

Our findings contrast with recent results from Zani et al., 2020, which report a strong influence of growing season photosynthesis on autumn senescence. The differences may result from several factors, including differences in the methods used, ecosystems focused on, and geographical and environmental patterns. First, the methods used in the two studies have notable differences. In Zani et al., 2020, the results were based on a model of growing season photosynthesis; in the present study, however, we used flux tower estimated GPP based on direct eddy covariance observations. Also, Zani et al., 2020 used phenology records from central Europe, while we use phenology estimates across a broad geographical range of boreal and temperate North America and Europe, made from multiple approaches (the flux-estimated, remotely sensed and ground observations at Harvard Forest).

In addition, the ecosystems of interest are different. In the present study, we focused on 8 different types of biomes across North America and Europe, while the Zani et al., 2020 study mostly focused on central Europe deciduous forests. The carry-over effects, especially the effects as predicted from the sink limitation hypothesis proposed as an explanation of their observations by Zani et al. (2020), are most likely to happen in ecosystems in which nutrients, water and/or sink capacity are more likely to be limiting factors (Fatichi et al., 2014). We did find, however, that growing season photosynthesis contributed marginally negatively to remotely sensed EOS in evergreen needleleaf forests when using the nighttime partitioning method (most of the ENF sites are in the boreal ecosystems where there might be sink limitations, see Fig. S2).

Finally, the geographical and environmental patterns for the sites tested in the two studies are also different. For instance, the soil nutrient availability of the Central Europe forests may be very different that of the other sites we tested (Ackerman et al., 2019).

4.2 The environmental controls over EOS in different ecosystems
We examined how the environmental variables in the autumn and in the previous seasons contributed to the changes of EOS in different ecosystems. Air temperature in summer and in

autumn were one of the most important factors that determined the EOS in different ecosystems (Fig. 3). This indicated that air temperature was contributing largely to the EOS in different ecosystems, similar to results found in Zhang et al., 2020. Also, we found that autumn VPD contributed negatively to the EOS timing, while the effects of summer VPD were mostly positive in different ecosystems. These results indicated that the water limitation possibly contributed to an earlier EOS.

At the same time, we found that the environmental controls over EOS could be different in different sites. For instance, in most ecosystems, the results indicated that the summer air temperature was negatively correlated with EOS in most ecosystems while we found a positive correlation in GRA sites. One possible explanation can be that the two GRA sites used in the present study (CA-Let, annual mean air temperature at 5.4 °C and IT-Mbo, annual mean air temperature at 5.1 °C) are both in cold regions and the warmer air temperature was usually associate with productive and lengthier growing season. To sum up, the environmental controls of EOS can be complex and different at different sites and in different ecosystems. Overall, we failed to find a negative carry-over effect of growing season photosynthesis on EOS.

Due to the complex controls on EOS in different ecosystems, future studies based on controlled experiments would be exceptionally beneficial. For instance, Zani et al., 2020 tested the hypothesis of sink limitation with three groups with different treatments and found that growing season photosynthesis had a negative relationship with the leaf senescence date. However, Norby et al., (2021) pointed out that in most FACE experiments, some of which also have a warming component, the leaf senescence dates in most experiments were either delayed or unchanged. Networks of phenological measurements such as PhenoCam (Richardson et al., 2018a) combined with flux measurement and or other experiments could also be of significance, especially for testing the sink limitation hypothesis (Richardson et al., 2018b).

4.3 Matches and mismatches between flux estimated and remotely sensed phenological metrics

Remote sensing of terrestrial ecosystem phenology is challenging, especially in ecosystems with low seasonality (e.g., ENF) or with significant snow presence (e.g., arctic tundra ecosystems). For instance, White et al., 2009 found that even when using the same input data sets, the derived remotely sensed phenological metrics are largely method dependent in Northern America. Also, Wu et al., 2017 found that the NDVI-estimated phenological metrics matched poorly with flux-tower estimated photosynthesis phenology metrics. Recently, Lu et al., 2018 found that satellite-observed SIF outperformed conventional VIs when estimating phenological metrics even with much coarser spatial resolutions at relatively homogeneous sites (~50 km). In the present study, we used the MODIS land dynamics product (MCD12Q2)

as it is one of the few publicly available datasets that have phenological metrics from satellite observations globally, and previous studies have shown that it effectively captures phenological dynamics (D'Odorico et al., 2015).

It is also worth noting that methods such as the double logistic curve fitting method to determine EOS used in this study assume that there is an inflection point within the time series of GPP. In the autumn, however, the senescence of photosynthesis can be more subtle, and the inflection points can be more difficult to detect. For instance, we found that the MODIS phenological metrics performed better in DBF sites where the inflection points were more significant. Overall, when comparing all sites, we found a significant relationship between flux-estimated and remotely sensed phenological metrics (Fig. S3).

We also compared the predictability of the two EOS metrics by using a linear regression model that used all predictors (Table 2). The results indicated that overall, in DBF, MF and GRA sites, the flux tower inferred EOS are more predictable than the MODIS phenology products; while in ENF, the remotely sensed metrics from MODIS are easier to predict. This may result from the subtle and slow changes of GPP in the fall in ENF sites. In summary, we argue that flux estimated and remotely sensed phenological metrics both contain meaningful information despite the mismatches in some cases.

Table 2. Comparison of predictability (R) of flux tower inferred and remotely sensed end of growing season EOS in deciduous broadleaf forest (DBF), evergreen needleleaf forest (ENF), mixed forest (MF), grassland (GRA) and ALL sites. Here, we used the International Geosphere-Biosphere Program (IGBP) scheme to identify the biome types of different sites, and the values in the table indicate the correlation between a multiple linear model prediction and observations in both models.

IGBP	DBF	ENF	MF	GRA	ALL
Tower EOS	0.47	0.27	0.49	0.82	0.21
MCD12Q2	0.49	0.33	0.25	0.81	0.18

5. Conclusion

We tested the relationships between growing season photosynthesis and estimates of leaf senescence and EOS in different ecosystems. We did not find negative carry-over effects of growing season photosynthesis on leaf senescence and EOS in most sites and most ecosystems, in contrast to recent reports. We also found that the controls of EOS in different ecosystems were different and, in most cases, a more productive growing season was related to a later, not earlier, leaf senescence. Our results challenge the notion that EOS is negatively affected by growing season photosynthesis, and highlight the need for controlled experiments to distinguish competing controls on the timing of fall senescence.

References

Ackerman, D., Millet, D. B., & Chen, X. (2019). Global estimates of inorganic nitrogen deposition across four decades. Global Biogeochemical Cycles, 33(1), 100-107.

Archetti, M., Richardson, A. D., O'Keefe, J., & Delpierre, N. (2013). Predicting climate change impacts on the amount and duration of autumn colors in a New England forest. *PLoS One*, *8*(3), e57373.

Baldocchi, D. (2008). 'Breathing'of the terrestrial biosphere: lessons learned from a global network of carbon dioxide flux measurement systems. *Australian Journal of Botany*, *56*(1), 1–26.

Buermann, W., Forkel, M., O'sullivan, M., Sitch, S., Friedlingstein, P., Haverd, V., Jain, A. K., Kato, E., Kautz, M., & Lienert, S. (2018). Widespread seasonal compensation effects of spring warming on northern plant productivity. *Nature*, *562*(7725), 110–114.

Chmielewski, F.-M., & Rötzer, T. (2002). Annual and spatial variability of the beginning of growing season in Europe in relation to air temperature changes. *Climate Research*, *19*(3), 257–264.

D'Odorico, P., Gonsamo, A., Gough, C. M., Bohrer, G., Morison, J., Wilkinson, M., Hanson, P. J., Gianelle, D., Fuentes, J. D., & Buchmann, N. (2015). The match and mismatch between photosynthesis and land surface phenology of deciduous forests. *Agricultural and Forest Meteorology*, *214–215*.

Delpierre, N., Dufrêne, E., Soudani, K., Ulrich, E., Cecchini, S., Boé, J., & François, C. (2009). Modelling interannual and spatial variability of leaf senescence for three deciduous tree species in France. *Agricultural and Forest Meteorology*, *149*(6–7), 938–948.

Falge, E., Baldocchi, D., Tenhunen, J., Aubinet, M., Bakwin, P., Berbigier, P., Bernhofer, C., Burba, G., Clement, R., & Davis, K. J. (2002). Seasonality of ecosystem respiration and gross primary production as derived from FLUXNET measurements. *Agricultural and*

Forest Meteorology, *113*(1–4), 53–74.

Fatichi, S., Leuzinger, S., & Körner, C. (2014). Moving beyond photosynthesis: from carbon source to sink driven vegetation modeling. *New Phytologist*, *201*(4), 1086–1095.

Finzi, A. C., Giasson, M. A., Barker Plotkin, A. A., Aber, J. D., Boose, E. R., Davidson, E. A., ... & Foster, D. R. (2020). Carbon budget of the Harvard Forest Long Term Ecological Research site: Pattern, process, and response to global change. Ecological Monographs, 90(4), e01423.

Friedlingstein, P., O'sullivan, M., Jones, M. W., Andrew, R. M., Hauck, J., Olsen, A., ... & Zaehle, S. (2020). Global carbon budget 2020. *Earth System Science Data*, *12*(4), 3269-3340.

Fu, Z., Stoy, P. C., Luo, Y., Chen, J., Sun, J., Montagnani, L., Wohlfahrt, G., Rahman, A. F., Rambal, S., Bernhofer, C., Wang, J., Shirkey, G., & Niu, S. (2017). Climate controls over the net carbon uptake period and amplitude of net ecosystem production in temperate and boreal ecosystems. *Agricultural and Forest Meteorology*, *243*, 9–18.

Gamon, J. A. (2015). Reviews and Syntheses: Optical sampling of the flux tower footprint. *Biogeosciences*, *12*(14), 4509–4523.

Ganguly, S., Friedl, M. A., Tan, B., Zhang, X., & Verma, M. (2010). Land surface phenology from MODIS: Characterization of the Collection 5 global land cover dynamics product. *Remote Sensing of Environment*, *114*(8), 1805–1816.

Gonsamo, A., Chen, J. M., Wu, C., & Dragoni, D. (2012). Predicting deciduous forest carbon uptake phenology by upscaling FLUXNET measurements using remote sensing data. *Agricultural and Forest Meteorology*, *165*, 127–135. https://doi.org/10.1016/j.agrformet.2012.06.006

Igolkina, A. A., & Meshcheryakov, G. (2020). semopy: A Python Package for Structural Equation Modeling. *Structural Equation Modeling: A Multidisciplinary Journal*, *27*(6), 952–963. https://doi.org/10.1080/10705511.2019.1704289

Jeong, S., HO, C., GIM, H., & Brown, M. E. (2011). Phenology shifts at start vs. end of growing season in temperate vegetation over the Northern Hemisphere for the period 1982–2008. *Global Change Biology*, *17*(7), 2385–2399.

Joiner, J., Yoshida, Y., Vasilkov, A. P., Schaefer, K., Jung, M., Guanter, L., Zhang, Y., Garrity, S., Middleton, E. M., Huemmrich, K. F., Gu, L., & Belelli Marchesini, L. (2014). The seasonal cycle of satellite chlorophyll fluorescence observations and its relationship to vegetation phenology and ecosystem atmosphere carbon exchange. *Remote Sensing of Environment*, *152*, 375–391.

Keenan, T. F., & Williams, C. A. (2018). The terrestrial carbon sink. *Annual Review of Environment and Resources*, *43*, 219–243.

Keenan, T. F., Gray, J., Friedl, M. A., Toomey, M., Bohrer, G., Hollinger, D. Y., Munger, J. W., O'Keefe, J., Schmid, H. P., & Wing, I. S. (2014). Net carbon uptake has increased through warming-induced changes in temperate forest phenology. *Nature Climate Change*, *4*(7), 598.

Keenan, T. F. & Richardson, A. D. (2015). The timing of autumn senescence is affected by the timing of spring phenology: implications for predictive models. *Global Change Biology*, *21*(7), 2634–2641.

Keenan, T. F., Moore, D. J., & Desai, A. (2019). Growth and opportunities in networked synthesis through AmeriFlux.

Körner, C., & Basler, D. (2010). Phenology under global warming. *Science*, *327*(5972), 1461–1462.

Lang, W., Chen, X., Qian, S., Liu, G., & Piao, S. (2019). A new process-based model for predicting autumn phenology: How is leaf senescence controlled by photoperiod and temperature coupling? *Agricultural and Forest Meteorology*, *268*, 124–135.

Lasslop, G., Reichstein, M., Papale, D., Richardson, A. D., Arneth, A., Barr, A., Stoy, P., & Wohlfahrt, G. (2010). Separation of net ecosystem exchange into assimilation and respiration using a light response curve approach: critical issues and global evaluation. *Global Change Biology*, *16*(1), 187–208.

Lian, X., Piao, S., Chen, A., Wang, K., Li, X., Buermann, W., Huntingford, C., Peñuelas, J., Xu, H., & Myneni, R. B. (2021). Seasonal biological carryover dominates northern vegetation growth. *Nature Communications*, *12, 983*.

Liu, Q., Fu, Y. H., Zhu, Z., Liu, Y., Liu, Z., Huang, M., Janssens, I. A., & Piao, S. (2016). Delayed autumn phenology in the Northern Hemisphere is related to change in both climate and spring phenology. *Global Change Biology*, *22*(11), 3702–3711.

Lu, X., Cheng, X., Li, X., & Tang, J. (2018). Opportunities and challenges of applications of satellite-derived sun-induced fluorescence at relatively high spatial resolution. *Science of The Total Environment*, *619–620*, 649–653.

Migliavacca, M., Sonnentag, O., Keenan, T. F., Cescatti, A., O'keefe, J., & Richardson, A. D. (2012). On the uncertainty of phenological responses to climate change, and implications for a terrestrial biosphere model. *Biogeosciences*, *9*(6), 2063-2083.

Miles, P. R. (2019). pymcmcstat: A python package for bayesian inference using delayed rejection adaptive metropolis. *Journal of Open Source Software*, *4*(38), 1417.

Norby, R. J. (2021). Comment on "Increased growing-season productivity drives earlier autumn leaf senescence in temperate trees." *Science*, *371*(6533).

Novick, K. A., Biederman, J. A., Desai, A. R., Litvak, M. E., Moore, D. J. P., Scott, R. L., & Torn, M. S. (2018). The AmeriFlux network: A coalition of the willing. *Agricultural and Forest Meteorology*, *249*, 444–456.

O'Keefe, J. (2019). *Phenology of woody species at Harvard Forest since 1990*.

Park, T., Ganguly, S., Tømmervik, H., Euskirchen, E. S., Høgda, K.-A., Karlsen, S. R., Brovkin, V., Nemani, R. R., & Myneni, R. B. (2016). Changes in growing season duration and productivity of northern vegetation inferred from long-term remote sensing data. *Environmental Research Letters*, *11*(8), 84001.

Pastorello, G., Trotta, C., Canfora, E., Chu, H., Christianson, D., Cheah, Y.-W., Poindexter, C., Chen, J., Elbashandy, A., & Humphrey, M. (2020). The FLUXNET2015 dataset and

the ONEFlux processing pipeline for eddy covariance data. *Scientific Data*, *7*(1), 1–27.

Piao, S., Friedlingstein, P., Ciais, P., Viovy, N., & Demarty, J. (2007). Growing season extension and its impact on terrestrial carbon cycle in the Northern Hemisphere over the past 2 decades. *Global Biogeochemical Cycles*, *21*(3).

Richardson, A D, Hufkens, K., Milliman, T., Aubrecht, D. M., Chen, M., Gray, J. M., Johnston, M. R., Keenan, T. F., Klosterman, S. T., Kosmala, M., Melaas, E. K., Friedl, M. A., & Frolking, S. (2018a). Tracking vegetation phenology across diverse North American biomes using PhenoCam imagery. *Sci Data*, *5*, 180028. https://doi.org/10.1038/sdata.2018.28

Richardson, A. D., Hufkens, K., Milliman, T., Aubrecht, D. M., Furze, M. E., Seyednasrollah, B., ... & Hanson, P. J. (2018b). Ecosystem warming extends vegetation activity but heightens vulnerability to cold temperatures. Nature, 560(7718), 368-371.

Richardson, A. D, Bailey, A. S., Denny, E. G., Martin, C. W., & O'KEEFE, J. (2006). Phenology of a northern hardwood forest canopy. *Global Change Biology*, *12*(7), 1174–1188.

Reichstein, M., Falge, E., Baldocchi, D., Papale, D., Aubinet, M., Berbigier, P., ... & Valentini, R. (2005). On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm. Global change biology, 11(9), 1424-1439.

Seddon, A. W. R., Macias-Fauria, M., Long, P. R., Benz, D., & Willis, K. J. (2016). Sensitivity of global terrestrial ecosystems to climate variability. *Nature*, *531*(7593), 229–232.

Song, Y., Linderholm, H. W., Chen, D., & Walther, A. (2010). Trends of the thermal growing season in China, 1951–2007. *International Journal of Climatology: A Journal of the Royal Meteorological Society*, *30*(1), 33–43.

Tang, J., Körner, C., Muraoka, H., Piao, S., Shen, M., Thackeray, S. J., & Yang, X. (2016). Emerging opportunities and challenges in phenology: a review. *Ecosphere*, *7*(8), e01436. https://doi.org/10.1002/ecs2.1436

van Vliet, A. J. H., de Groot, R. S., Bellens, Y., Braun, P., Bruegger, R., Bruns, E., Clevers, J., Estreguil, C., Flechsig, M., & Jeanneret, F. (2003). The European phenology network. *International Journal of Biometeorology*, *47*(4), 202–212.

White, M. A., de Beurs, K. M., Didan, K., Inouye, D. W., Richardson, A. D., Jensen, O. P., O'KEEFE, J., Zhang, G., Nemani, R. R., & van Leeuwen, W. J. D. (2009). Intercomparison, interpretation, and assessment of spring phenology in North America estimated from remote sensing for 1982–2006. *Global Change Biology*, *15*(10), 2335–2359.

Wu, C., Peng, D., Soudani, K., Siebicke, L., Gough, C. M., Arain, M. A., Bohrer, G., Lafleur, P. M., Peichl, M., Gonsamo, A., Xu, S., Fang, B., & Ge, Q. (2017). Land surface phenology derived from normalized difference vegetation index (NDVI) at global FLUXNET sites. *Agricultural and Forest Meteorology*, *233*, 171–182. https://doi.org/10.1016/j.agrformet.2016.11.193

Wutzler, T., Lucas-Moffat, A., Migliavacca, M., Knauer, J., Sickel, K., Šigut, L., Menzer, O., & Reichstein, M. (2018). Basic and extensible post-processing of eddy covariance flux data with REddyProc. *Biogeosciences*, *15*(16), 5015–5030.

Yang, L., & Noormets, A. (2021). Standardized flux seasonality metrics: a companion dataset for FLUXNET annual product. *Earth System Science Data*, *13*(4), 1461–1475.

Yu, Z., Liu, S., Wang, J., Sun, P., Liu, W., & Hartley, D. S. (2013). Effects of seasonal snow on the growing season of temperate vegetation in China. *Global Change Biology*, *19*(7), 2182–2195.

Zani, D., Crowther, T. W., Mo, L., Renner, S. S., & Zohner, C. M. (2020). Increased growing-season productivity drives earlier autumn leaf senescence in temperate trees. *Science*, *370*(6520), 1066–1071.

Zhang, X., Friedl, M. A., & Schaaf, C. B. (2006). Global vegetation phenology from Moderate Resolution Imaging Spectroradiometer (MODIS): Evaluation of global patterns and comparison with in situ measurements. *Journal of Geophysical Research: Biogeosciences*, *111*(G4).

Zhang, X., Friedl, M. A., Schaaf, C. B., Strahler, A. H., Hodges, J. C. F., Gao, F., Reed, B. C., & Huete, A. (2003). Monitoring vegetation phenology using MODIS. *Remote Sensing of Environment*, *84*(3), 471–475.

Zhang, Y., Commane, R., Zhou, S., Williams, A. P., & Gentine, P. (2020). Light limitation regulates the response of autumn terrestrial carbon uptake to warming. *Nature Climate Change*, *10*(8), 739–743.

Zhang, Y., Zhou, S., Gentine, P., & Xiao, X. (2019). Can vegetation optical depth reflect changes in leaf water potential during soil moisture dry-down events? *Remote Sensing of Environment*, *234*.