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Declining precipitation frequency drives earlier leaf senescence by intensifying drought stress and enhancing drought acclimation

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Abstract: Precipitation is an important factor influencing the date of leaf senescence (DFS), which in turn affects carbon uptake of terrestrial ecosystems. However, the temporal patterns of precipitation frequency ($P_{freq}$) and its impact on DFS remain largely unknown. Using both long-term carbon flux data and satellite observation of DFS across the Northern Hemisphere, here we show that, after excluding impacts from of temperature, radiation and total precipitation, declining $P_{freq}$ drives earlier DFS from 1982 to 2022. A decrease in $P_{freq}$ intensified drought stress by reducing root-zone soil moisture and increasing atmospheric dryness, and limit the photosynthesis necessary for sustained growth. The enhanced drought acclimation also explained the positive $P_{freq}$-DFS relationship. We found plants experiencing decreased $P_{freq}$ showed a more rapid response to drought, as represented by a shorter drought response lag, a measure of the time between a drought event and the most severe reduction in vegetation growth. In particular, increased evapotranspiration with shorter drought response lag was observed, further implying an enhanced water acquisition strategy representing drought acclimation as showing in strengthening roots system to deeper water resources. Finally, we found current state-of-art Earth system models largely failed to capture the sensitivity of DFS to changes in $P_{freq}$ and incorrectly predicted the direction of correlations for approximately half of the northern global lands, in both historical simulations and future predictions under various shared socioeconomic pathways (SSPs). Our results therefore highlight the critical need to include precipitation frequency, rather than just total precipitation, into models to accurately forecast plant phenology under future climate change.
Plant phenology is greatly affected by ongoing changing climate. While warming typically leads to earlier spring leaf-out, predicting temporal changes in the dates of autumn leaf senescence (DFS) is more complex due to the various drivers involved, leading to mixed observations and model predictions of either earlier or later DFS across northern terrestrial ecosystems. For example, rising temperatures late in the season can delay DFS given sufficient water availability. Conversely, warmer conditions can also speed up seasonal development, resulting in earlier DFS. Moreover, water availability plays a crucial role in autumn phenology, with severe droughts causing earlier DFS. Thus, understanding the impact of water availability on DFS changes is becoming increasingly vital in the context of climate change, especially with the expectation of more frequent and severe droughts in the future.

Precipitation is essential for plant growth, particularly through the replenishment of soil moisture. However, its impact on DFS varies widely, with both positive and negative effects reported. This inconsistency is likely due to local environmental factors, such as the amount of annual precipitation, and geophysical conditions like topography. The complexity of these patterns and the lack of a clear understanding of the underlying processes make it challenging to accurately model the effects of precipitation on DFS. We propose that the focus should not be solely on the amount of precipitation but also on its temporal patterns, such as frequency. Emerging evidence suggests that variations in the timing and intensity of precipitation can greatly impact plant growth. Therefore, we
aimed to explore the responses and the underlying reasons of DFS to changes in precipitation frequency across the Northern Hemisphere. To this end, we used both long-term flux measurements and satellite observations (Figure S1, Table S1-S2), combined with precipitation frequency data from gridded meteorological datasets (both ERA5 and CRU) (Figure S2). Additionally, we evaluated the capability of current state-of-the-art Earth system models to reproduce the observed relationships between DFS and precipitation frequency (Figure S3, Table S3-S4).

Results

We observed a widespread decline in $P_{freq}$ across the Northern Hemisphere between 1982 to 2022 from both the ERA5 and CRU data (Figure S4). By controlling autumn temperature and radiation, we observed negative correlations between DFS and total precipitation at higher latitudes (>50 degrees), whereas positive correlations between DFS and precipitation were more common at lower latitudes (Figure 1A). Overall, the proportions of significantly negative and positive DFS-precipitation correlations were 15.6% and 9.5%, respectively. These proportions slightly changed to 17.4% vs. 8.8% when accounting for the effects of precipitation frequency using partial correlation (Figure 1B).

In comparison, $P_{freq}$ was mostly positively correlated with DFS, with 57.7% of correlations being positive and 14.9% being significantly positive, about double the proportion of significant negative correlations (7.8%) (Figure 1C). Further analysis, illustrated in a Sankey diagram, showed that considering the impact of $P_{freq}$ significantly reduced the strength of negative DFS-precipitation relationships. This trend remained consistent...
across different plant functional types (Figure 1 E). We also plotted the distributions of the
total precipitation-DFS and P_{freq}-DFS correlations in the total precipitation and frequency
space (Extended Figure 1). We found earlier DFS with increased total precipitation often
occurred when precipitation frequency exceeded an empirical threshold of 15. In
comparison, the positive correlations between precipitation frequency and DFS were
overall broadly consistent, and earlier DFS with increased frequency was observed only
for low precipitation frequency but with extreme total precipitation. Flux measurements
showed similar patterns: The correlation between PF and DFS was predominantly positive
(23.1% positive vs. 5.7% negative, Figure 1 F), whereas the correlation between P_{freq} and
DFS was equally positive and negative (15.8% positive vs. 15.3% negative).
Figure 1. Relationships between the dates of leaf senescence (DFS) and precipitation changes. A represents the partial correlations between DFS and total precipitation, controlling only temperature and radiation, and B by additionally controlling precipitation frequency. C is partial correlations between DFS and precipitation frequency, controlling temperature, radiation and total precipitation. D shows the changes between significant positive and negative correlations with the Sankey diagram. E represents the results classified by plant functional types (See methods). F shows the same analysis using flux measurements. P and N represent positive and negative, respectively. Significance was set with p<0.05.
We used a structural equation model (SEM) to explore the underlying mechanisms that may explain the predominantly positive correlation between $P_{\text{freq}}$ and DFS (Figure 2 A). We found that both total precipitation and $P_{\text{freq}}$ significantly decreased radiation (path effect of -0.42, -0.43, respectively). In comparison, root zone soil moisture was more strongly affected by $P_{\text{freq}}$ than by total precipitation (0.50 vs. 0.44, $P<0.01$). In particular, atmospheric dryness increased significantly with declined $P_{\text{freq}}$ than with total precipitation, with path effects of -0.51 ($P<0.01$) and -0.35 ($P<0.05$), respectively. This suggests that declines in precipitation frequency have a more severe impact on plant drought stress than changes in total precipitation, which in turn causes earlier leaf senescence in many regions.

We also found a significantly positive relationship between $P_{\text{freq}}$ and the drought response lag ($R^2=0.40$, $p<0.05$), indicating that plants acclimate to drought more quickly with decreased $P_{\text{freq}}$, necessitating longer recovery times from drought ($R^2=0.82$, $p<0.05$, Figure 2 B-C). Using a moving window approach, we observed an increasing importance of $P_{\text{freq}}$ in regulating DFS changes over the past four decades, indicated by increases in the slope values (Figure 2 D). We further found that decreased $P_{\text{freq}}$ was often associated with a smaller size of a single rain event (11.7% and 0.9% for positive and negative correlations, respectively), reducing soil moisture accumulation (Figure 2 E) and thereby contributing to the increased soil moisture variability and earlier DFS consequently ($R^2=0.64$, $P<0.01$, Figure 2 F).
Figure 2. Mechanisms for the correlation between precipitation frequency and the dates of leaf senescence (DFS). A shows the structural equation model (SEM) analysis. B and C represent the changes of drought response lag and drought recovery time with precipitation frequency. D shows the moving window approach with respect of positive and negative sensitivities of DFS to precipitation frequency over 1982-2022 (see Methods). E shows the relationship between precipitation frequency and the maximum daily precipitation size (N and P represent negative and positive correlations). F represents the correlation between DFS and root zone soil moisture variability using coefficients of variation (%). * and ** represent $p<0.05$ and $p<0.01$, respectively.
We further tested if the positive impacts of $P_{\text{freq}}$ on DFS could be reproduced by current state-of-the-art Earth system models. This included both Trendy models for historical simulations and CMIP6 models for future projections under various shared socioeconomic pathways (SSPs), including SSP126, SSP245, SSP370, and SSP585. We found that Trendy models overall captured the relationship between DFS and precipitation frequency, with larger proportions of significant positive correlations (Figure 3 A). Similarly, among the 14 CMIP6 models, only three failed to reproduce the observed patterns (ACCESS-ESM1-5, BCC-CSM2-MR and TaiESM1). However, when assessing the sensitivity of DFS to changes in $P_{\text{freq}}$ (i.e., how DFS changes per unit variation in $P_{\text{freq}}$), we observed substantial differences among models (Figure 3 B). Only seven out of 16 Trendy models demonstrated positive sensitivities, and even fewer CMIP6 models showed positive sensitivities. Additionally, we assessed the accuracy of these models in predicting the sign of the DFS-$P_{\text{freq}}$ relationship at each pixel level, comparing these predictions with observations (Figure 3 C). About half of all pixels showed mismatches, highlighting the models' limited accuracy in capturing the DFS-$P_{\text{freq}}$ correlations.
Figure 3. The test of Earth system models in reproducing the observed relationship between the dates of leaf senescence (DFS) and precipitation frequency. A shows the overall proportions of significant positive and negative correlations. B represents the sensitivity of DFS to precipitation frequency changes. C is the comparison on the signs of correlation for each pixel. Four shared socioeconomic pathways (SSPs) were included for CMIP6 models, including SSP126, SSP245, SSP370, and SSP585, respectively). -- and ++ represent consistent negative and positive observations. Significance was set with p<0.05.
Discussion

Our research has revealed a positive correlation between DFS and $P_{freq}$. Accordingly, the widespread declines in the $P_{freq}$ over the past four decades have led to earlier DFS in northern ecosystems. The impact of these changes varies among plant functional types, reflecting the diversity of strategies plants use to adapt to local environments and respond to climate change factors$^{17-18}$. Limited soil moisture due to reduced $P_{freq}$ can cause drought stress, negatively affecting soil organic carbon (SOC) levels and soil respiration$^{19-20}$. Conversely, excessive moisture can also hinder respiration by reducing oxygen availability, which may explain observations of earlier DFS in regions with increased precipitation$^{21}$. The interaction between soil moisture, heat, SOC, soil microorganisms, as well as soil geochemical characteristics defines the optimal conditions for plant growth$^{22-23}$. These conditions are the result of long-term adaptation strategies developed by plants. Changes in $P_{freq}$ alter these soil properties and this may prompt plants to adjust their DFS to enhance survival in changing environments. This adjustment may also reflect the increased demand for soil resources, particularly soil moisture, to sustain photosynthetic activity in a warming climate. Overall, our findings underscore the importance of considering seasonal precipitation patterns, rather than just total amounts, in understanding leaf senescence timing. This insight is crucial for incorporating temporal changes in precipitation into future ecosystem models to better understand the impacts of climate change on plant phenology and growth.

In our study, we aimed to elucidate the mechanisms behind the observed trend of
earlier DFS with decreased $P_{freq}$, a task complicated by the interactive effects of precipitation amount and variability on terrestrial ecosystem processes$^{34}$. Using partial correlation and SEM techniques, we identified that the primary driver for earlier DFS under reduced $P_{freq}$ may be the intensified water constraints on photosynthesis through significant reductions in root-zone moisture and increases in VPD. A lower frequency of rainfall events implies longer drought periods. Consequently, soil moisture gradually declines, particularly in the surface layers where the majority of a plant's roots are concentrated. This poses a challenge for plants to access adequate water supply, especially after prolonged drought periods. Experimental studies have indicated that plant photosynthesis and primary productivity are significantly impacted by changes in $P_{freq}^{15}$. Reduced $P_{freq}$, often coupled with smaller precipitation events, adversely affects soil moisture recharge and increases soil moisture variability, which in turn drives earlier leaf senescence. The increase in atmospheric dryness further accelerates the cessation of photosynthesis.

A pivotal finding of our research is the identification of a significantly shortened drought response lag associated with decreased $P_{freq}$, a process representing drought acclimation. In particular, we found a significant negative correlation between drought response lag and evapotranspiration (ET) (Extended Figure 2 A). Such results implies an enhanced water-use strategy of plants that further supports plant adaptation and acclimation, probably by strengthening the growth of root systems to extend downstream for deeper water sources under droughts$^{25}$. This reason has been supported by our results showing
increased root depth with lower drought response lag (Extended Figure 2B). The enhanced drought acclimation is likely linked to the adaptive strategy of plants that have been exposed to prolonged periods of drought, including more effective water management and utilization. Plants can rapidly reduce water loss or increase water uptake when water availability is scarce through morphologically deeper roots and an enhanced tolerance to drought physiologically by accumulating osmoprotectants and other regulatory substances. Our observations, encompassing a wide range of species with varied plant functional types and local climatic backgrounds, therefore confirm and extend the critical role of $P_{freq}$ on vegetation growth beyond site-level experiments.

We show that while current Earth system models were able to reproduce the overall trend in the correlation between DFS and $P_{freq}$, they inaccurately represent the sensitivity of DFS to changes in $P_{freq}$. A pixel-by-pixel analysis showed that these models incorrectly predict the sign of the DFS- $P_{freq}$ correlation for half of the regions examined. This discrepancy may be primarily due to the models’ reliance on the link between total precipitation and soil moisture, overlooking the significant effects of $P_{freq}$ on ecosystem functions. However, the timing, frequency and duration of precipitation events are determinants of ecosystem processes during autumn and therefore important for leaf senescence, as shown by our observations. Therefore, current Earth system models, driven by basic conceptual frameworks that ignore the effects of $P_{freq}$ on plant hydraulics, fall short in reproducing the temporal effects of $P_{freq}$ on DFS. Including $P_{freq}$—a key measure of precipitation variability—into ecosystem models therefore has large potential
to improve future predictions of drought impacts on ecosystems, especially given the expectation that future droughts will intensify in several dimensions, including magnitude, duration, timing, and frequency\textsuperscript{11,31}.

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Methods

1. Study area

Northern Hemisphere (NH) encompasses a wide range of ecosystems that are essential for maintaining the global carbon balance and limiting global warming. Monitoring the dynamics of vegetation in the NH is crucial for understanding and mitigating climate. In this study, we focused on middle and high latitude regions of Northern Hemisphere (>30°N), where vegetation dynamic has an evident seasonality (Figure S1).

2. Site-level DFS from flux data

The site-level phenology observations were derived from daily gross primary productivity (GPP) based on the eddy-covariance flux measurements. We removed sites with insufficient observations (< 8 yr). As a result, 52 flux sites with a total of 662 year-site records of daily GPP from the FLUXNET database were selected (Table S2). We used a dynamic threshold of 10% of the annual maximum GPP to determine DFS.

3. Satellite derived DFS

The long time series of continuous NDVI dataset from the GIMMS-3G+ product was used to derive DFS. This dataset was based on corrected and calibrated measurements from Advanced Very High Resolution Radiometer (AVHRR) data with a spatial resolution of 0.0833 degree and a half-month interval for 1982 to 2022.
To better capture the seasonal signals of vegetation while eliminating the interference of atmospheric effects and snow cover, the NDVI time series was first reconstructed by weighted Whittaker algorithm\textsuperscript{33}. Then a seven-parameter double logistic function\textsuperscript{34} was used to fit the NDVI time series and DFS was determined based on inflection method\textsuperscript{35}.

\[ f(t) = m_1 + (m_2 - m_7 \cdot t) \left( \frac{1}{1 + e^{(m_3 - t)/m_4}} - \frac{1}{1 + e^{(m_5 - t)/m_6}} \right) \quad (1) \]

where, \( m_1 \) is background NDVI; \( m_2 \) is the difference between summer-time NDVI and background value; \( m_3 \) and \( m_5 \) are the midpoints in the days of the year of the transitions of spring green-up and autumn senescence, respectively; \( m_4 \) and \( m_6 \) are normalized slope coefficients for these transitions; \( m_7 \) is summer green-down parameter. DFS was defined as the time when the curvature changing rate reached its last local maximum value.

4. Simulated DFS from Trendy and CMIP6

We simulated DFS based on output GPP from 16 Trendy models during 1983–2021 and 14 CMIP6 models under different shared socioeconomic pathways (SSP-126, SSP-245, SSP-370, and SSP-585) during 2016–2100 (Table S3). DFS was determined using the same inflection method as the NDVI-based DFS.

5. Climate data

We derived monthly total amount (\( P_{\text{total}} \)) and frequency (\( P_{\text{freq}} \)) of precipitation from two independent datasets: 1) the Climatic Research Unit Time-Series (CRU TS 4.07) and 2) the fifth generation European Centre for Medium-Range Weather Forecasts reanalysis of
the global climate (ERA5). The CRU dataset is produced by the interpolation from extensive networks of climatic station observations and provides several climate variables on a 0.5° × 0.5° spatial resolution and a monthly temporal resolution\textsuperscript{36}. We used wet day frequency, which defined as days with ≥0.1 mm precipitation, as $P_{\text{freq}}$. The ERA5 product provides hourly estimates of various climate variables with a spatial resolution of 0.1° based on vast amounts of historical observations\textsuperscript{37}. We obtained total precipitation from the monthly aggregated datasets and calculated the number of rainy days per month based on the daily precipitation (≥0.1 mm). We used the mean value of $P_{\text{total}}$ and $P_{\text{freq}}$ from CRU and ERA5 as final $P_{\text{freq}}$ and $P_{\text{total}}$ for 1982–2022 to reduce the uncertainty from a single dataset. Monthly mean temperature was obtained from CRU and surface net solar radiation was accessed from ERA5. Vapor pressure deficit (VPD) and evapotranspiration (ET) data for 1982–2022 were obtained from TerraClimate with a monthly temporal resolution and a 1/24 degree spatial resolution. The monthly root-zone soil moisture from 1982 to 2022 was obtained from Global Land Evaporation Amsterdam Model (GLEAM) with a spatial resolution of 0.25°.

6. Identification of drought events, drought recovery and drought response lag

Drought response lag and recovery time were obtained from Li et al. (2023)\textsuperscript{2}. Extreme drought events were identified by examining monthly SPEI-3 (Standardized Precipitation-Evapotranspiration Index at a 3-month scale) values below the threshold of -2. Drought recovery is defined as the duration (months) starting from the month with the deepest suppression of NDVI to the month when NDVI returns to within 95% of the
long-term average baseline in each pixel. The monthly SPEI3 and NDVI time series were first smoothed by a 3-month forward moving window, they were then sequentially deseasonalized and linearly detrended. To avoid lengthening the drought recovery duration due to algorithm design, if vegetation recovery extending through the dormant season and into subsequent year, the drought recovery was calculated as the total length of the recovery period minus the length of the dormant season. We measured response lag in months, which is the time between the lowest SPEI3 value and the most significant drop in NDVI caused by drought. We calculated both drought response lag and recovery time for each pixel individually.

7. Analysis

Precipitation, along with temperature and radiation, collectively regulate DFS. In addition, covariate effects exist among these climatic variables as well. Therefore, we applied partial correlation analysis to explore the impacts of $P_{\text{total}}$ and $P_{\text{freq}}$ on DFS. We performed partial correlation analysis under three scenarios: (1) partial correlation between DFS and $P_{\text{total}}$, removing the effects of temperature and radiation (scenario 1); (2) partial correlation between DFS and $P_{\text{total}}$, removing the effects of temperature, radiation, and $P_{\text{freq}}$ (scenario 2); (3) partial correlation between DFS and $P_{\text{freq}}$, removing the effects of temperature, radiation, and $P_{\text{total}}$ (scenario 3). According to previous studies, preseason forcings have a better predictive strength on phenology than fixed seasonal climate forcing alone. We thus used the preseason mean values of each climatic variable in the partial correlation analysis. For example, the preseason length of $P_{\text{freq}}$ was defined as
the period when the absolute value of partial correlation coefficient between $P_{\text{freq}}$ and DFS was at its maximum. For each pixel, the preseason periods of 0 to 6 months prior to the multi-year mean DFS were examined (Figure S5).

To investigate the temporal changes in the sensitivity of DFS to $P_{\text{freq}}$, we used a moving window method. We conducted tests on a variety of window sizes, ranging from 10 to 20 years. For each window size, we calculated the sensitivity of DFS to $P_{\text{freq}}$ based on multilinear regression within each moving window. Then we calculated the percentages of significant sensitivity ($P < 0.05$) and fitted these values to obtain the optimal window size with the largest $R^2$. As a result, the optimal window size was set as 19 years to perform subsequent analyses (Figure S6).

$$DFS = a \cdot P_{\text{freq}} + b \cdot P_{\text{total}} + c \cdot \text{Temperature} + d \cdot \text{Radiation} + \varepsilon$$

where, $a$, $b$, $c$ and $d$ are regression coefficients and represent the sensitivity of DFS to $P_{\text{freq}}$, $P_{\text{total}}$, temperature, and radiation, respectively. $\varepsilon$ is the residual error. All the climate variables used in the regression were the mean values during preseason.

To explore the potential mechanisms by which precipitation affects DFS, we performed structural equation modeling. Considering that precipitation patterns may affect DFS by influencing solar radiation and drought conditions, we selected radiation, VPD, and root-zone soil moisture to construct structural equation model.
References


Data availability

All data used in this study are available online. The specific links for each dataset are presented in Supplementary Tables S1.

Code availability

All data analyses and modeling were performed using Python and R. The codes for the phenological models are available at https://doi.org/10.5281/zenodo.5829780.

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Extended Figure 1. Spatial distribution of the correlation coefficients ($R^2$) with respect to total precipitation and its frequency. (a) Total precipitation ($P_{total}$) and dates of leaf senescence (DFS). (b) Precipitation frequency ($P_{freq}$) and DFS.
Extended Figure 2. Relationships between drought response lag and (A) evapotranspiration, and (B) root depth.
Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- ExtendedFigure1.jpg
- ExtendedFigure2.jpg
- Supplementaryinformation.pdf