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Field evidences for the positive effects of aerosols on tree growth

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Abstract

Theoretical and eddy covariance studies demonstrate that aerosol-loading stimulates canopy photosynthesis, but field evidence for the aerosol effect on tree growth is limited. Here, we measured in situ daily stem growth rates of aspen trees under a wide range of aerosol-loading in China. The results showed that daily stem growth rates were positively correlated with aerosol-loading, even at exceptionally high aerosol levels. Using structural equation modeling analysis, we showed that variations in stem growth rates can be largely attributed to two environmental variables covarying with aerosol loading: diffuse fraction of radiation and vapor pressure deficit (VPD). Furthermore, we found that these two factors influence stem growth by influencing photosynthesis from different parts of canopy. Using field observations and a mechanistic photosynthesis model, we demonstrate that photosynthetic rates of both sun and shade leaves increased under high aerosol-loading conditions but for different reasons. For sun leaves, the photosynthetic increase was primarily attributed to the concurrent lower VPD; for shade leaves, the positive aerosol effect was tightly connected with increased diffuse light. Overall, our study provides the first field evidence of increased tree growth under high aerosol loading. We highlight the importance of understanding biophysical mechanisms of aerosol-meteorology interactions, and incorporating the different pathways of aerosol effects into earth system models to improve the prediction of large-scale aerosol impacts, and the associated vegetation-mediated climate feedbacks.

KEYWORDS
aerosol loading, aerosol-meteorology interactions, canopy photosynthesis, diffuse radiation, mechanistic photosynthesis model, sun/shade leaf, tree stem growth, vapor pressure deficit

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1 | INTRODUCTION

Rapid economic growth has led to the emission of a large amount of particle matter into the atmosphere, which induces a dramatic increase in atmospheric aerosols, especially in East and South Asia (Hsu et al., 2012; Yoon et al., 2014). Mean annual aerosol loading in these regions has increased by 1.2–1.8 times in the past decade (Yoon et al., 2014) and has become one of the most serious air quality problems. Aerosols have strong impacts on the interactions between the biosphere and the atmosphere, not only by altering the earth's surface energy budget, but also by mediating feedbacks between vegetation and climate (IPCC, 2013; Mahowald et al., 2011; Mercado et al., 2009). Both eddy covariance and model studies suggest that intermediate increase in aerosol loading generally enhances ecosystem carbon uptake (Cirino, Souza, Adams, & Artaxo, 2014; Cohan, Xu, Greenwald, Bergin, & Chameides, 2002; Gu et al., 2003; Knohl & Baldocchi, 2008). Plant growth is a key indicator of the plant carbon uptake which would presumably increase under aerosol loadings. However, previous dendrochronology analysis often found no enhancement of tree-ring growth under historical aerosol increase due to major volcanic activities (Krakauer & Randerson, 2003; Mann, Fuentes, & Rutherford, 2012); thus, in situ observations on plant growth response to aerosol variations become necessary to understand whether plant growth also increases under aerosol loadings (Krakauer & Randerson, 2003; Mann et al., 2012; Rocha, Goulden, Dunn, & Wofsy, 2006).

Aerosol can influence plant physiological processes through multiple pathways. First, aerosol-loading can reduce total solar radiation reaching the canopy. Second, the fraction of diffuse radiation, however, can increase under aerosol-laden skies, resulting in more sunlight penetrating tree canopy and alleviating the strong light limitation of inner canopy. This has been referred to as the diffuse radiation fertilization effect (Kanniah, Beringer, North, & Hutley, 2012; Mercado et al., 2009; Roderick, Farquhar, Berry, & Noble, 2001). Third, high aerosol loading is often concurrent with low vapor pressure deficit (VPD) (Cirino et al., 2014; Gu et al., 2002; Wu, Guan, et al., 2017). This is because high aerosol optical depth (AOD) could decrease VPD through the cooling effect. On the other hand, high air humidity under low VPD condition could increase AOD because of the hygroscopic growth of particles (Ebert, Inerle-Hof, & Weinbruch, 2002; Hussein et al., 2006). Lower VPD can stimulate stomatal conductance and thus enhance canopy photosynthesis (Collatz, Ball, Grivet, & Berry, 1991; Moriana, Villalobos, & Fereres, 2002). This effect of the covarying meteorological conditions can be as important as the diffuse radiation fertilization effect (Steiner & Chameides, 2005) and contributes to the sensitivity of ecosystem carbon exchanges to aerosols (Wohlfahrt et al., 2008). Understanding how these pathways affect the physiological responses of growth and photosynthesis is crucial for predicting the effects of aerosol on vegetation dynamics and the ecosystem carbon cycle. Therefore, analysis of field observations of aerosol loading, meteorological conditions, plant growth, and photosynthesis at finer temporal (i.e., hourly and daily) scale can add more direct insights for better understanding the aerosol impacts. However, because manipulating aerosol loading in the field is challenging, few field observations have been made at leaf- and individual tree-scale, especially under exceptionally high aerosol-loading.

China is suffering severe aerosol pollution. Aerosol loading in the Beijing metropolitan area has a 4 to 7 days cycle of clean-to-polluted conditions (Guo et al., 2014), with AOD varying over a large range (0.1–1.9) on cloudless days. The chronic elevated but also highly fluctuating aerosol levels there provide a unique opportunity for studying how tree stem growth and leaf photosynthesis respond to different aerosol levels. In this study, we conduct four-year intensive field campaigns (2012–2015) in Beijing, China, to examine the response of aspen (*Populus euramericana* Neva.) to aerosols at tree and leaf levels. Instead of using AOD indirectly from MODIS products or Aerosol Robotic Network (AERONET) (Cirino et al., 2014; Doughty, Flanner, & Goulden, 2010; Niyogi et al., 2004; Oliveira et al., 2007; Yamasoe et al., 2006), we conduct in situ, real-time measurements of AOD along with the measurements of other meteorological variables. We estimated stem daily growth rates based on the field records of automatic dendrometer sensor measurements. We also measured the photosynthesis of sun-grown and shade-grown leaves under a controlled condition and estimated leaf and canopy photosynthesis with real-time metrological variables through mechanistic models. Here, we aim to leverage these intensive field observations to firstly evaluate whether the positive aerosol effect on stem growth holds in our study area under an exceptional wide range of aerosol loading, and then explore the potential mechanisms responsible for the observed pattern.

2 | MATERIALS AND METHODS

2.1 | Site description and experiment design

This study was conducted at the Beijing Forest Experimental Station of the Institute of Botany, Chinese Academy of Sciences (39.98° *N*, 116.20° *E*), Xiangshan, Beijing, China. The climate at this study site is a typical temperate continental monsoon climate with mean annual air temperature of 13°C and mean annual precipitation of 538 mm. The experimental plots were established in late March, 2011. Six 1×1 m^2 plots were arranged in 2 columns × 3 rows with a 0.5 m buffer zone between plots. One aspen (*Populus euramericana* Neva.) cutting was planted in each plot in early April, 2011. To exclude the confounding influence of cloud cover, field-based ecophysiological measurements of plant and meteorological factors were conducted only during cloud-free days. Two criterions were used to avoid the cloud contamination: first, There was no visible cloud which blocking the sun in the sky when we conducted field measurement; second, before we took measurements for plants, we conducted three continuous measurements of AOD with hand-held sunphotometer within 1-min period at about 20-s intervals. If AOD range within the triplet is lower than 0.03, we consider the atmosphere is cloud-free (Smirnov, Holben, Eck, Dubovik, & Slutsker, 2000).

2.2 | Aerosol loading and meteorological conditions

Aerosol optical depth (AOD) at 500 nm was measured with MICROTOPS II hand-held sunphotometer (Solar Light Inc., USA) every 30 min between 9:00 and 11:30 during the growing seasons in 2012 and 2013, and between 9:00 and 17:00 in 2014, and every 60 min between 9:00 and 17:00 in 2015.

During growing seasons of 2012 and 2013, total incident photosynthetic active radiation (PAR) in the open field and inner canopy was measured using a Li-Cor Quantum Sensor (LICOR Inc., USA) at a horizontal position when the leaf-level measurements were conducted, which represented the light condition for sun and shade leaves, respectively. Hourly observations of air temperature and air relative humidity (RH) were acquired from records of a nearby weather station.

An in situ meteorological monitoring system (Decagon Devices Inc., USA) and SPN1 Sunshine Pyranometer (Delta-T Devices Ltd, UK) were installed at the study site in May 2014, which enabled continuous monitoring of air temperature, RH, PAR, total solar radiation, and diffuse radiation at 30-min intervals. Vapor pressure deficit (VPD) was calculated based on the measured air temperature and RH.

2.3 | Responses of plant growth

We selected four trees in our experiment plots in May, 2014, and installed dendrometer sensors (DC3, Ecomatik, Germany) at the breast height (1.3 m). The stem diameters were continuously monitored and automatically recorded by a data logger (DL 15, Ecomatik, Germany) at half-hour intervals. Aspen stem daily growth (mm^2 day^{-1}) was defined as the difference in the stem sectional area at 11:30 p.m. (midnight) between two consecutive days, and daily shrinkage was defined as the difference between the highest and lowest stem sectional areas within the same day (see examples as shown in Figure S1). To avoid the confusion of cloud, we only used the observations on clear and windless days from June to August in 2014 and 2015. When evaluating the relationships between the daily stem growth, AOD, and VPD, these variables were detrended by removing the first-order autocorrelative term from the time-series (using the difference in values from one day to the next), to minimize the influence of seasonal changes.

2.4 | Responses of leaf photosynthesis

The leaf photosynthesis rates of sun and shade leaves were measured in situ between 9:00 and 11:30 on clear and windless days from June to September in 2012 and 2013. To avoid the confounding effects of phenology on leaf photosynthesis, we only use the measurements from July to August in the current analysis. Sun leaves referred to fully expanded, recently matured and healthy leaves located in the third or fourth position from top of an unshaded branch located in the middle part of the canopy. Shade leaves referred to fully matured, healthy and completely shaded leaves located in the basal part of the canopy. For each aspen tree, we randomly selected three sun leaves under sunlit condition and three shade leaves under shaded condition located in different branches to measure their photosynthesis. Averaged values of these three leaves were used to represent sun or shade leaf response of this tree under different aerosol loadings, respectively. The measurements were conducted using a LI-6400 (LICOR Inc., USA) with a standard leaf chamber under a saturated light (1,500 μmol m^{-2} s^{-1} PPFD, supplied by a red-blue LED light source) and a controlled temperature (30°C chamber temperature) environment. The leaf chamber was in the horizontal position when measuring. Measurements usually stabilized in 3 min after clamping the leaf in the chamber. The photosynthesis rates (under saturated PAR and constant temperature, A_n) were logged when fluxes were stable over 10 s.

Using Farquhar, von Caemmerer and Berry (FvCB) approach (Farquhar, Caemmerer, & Berry, 1980) coupled with Medlyn stomatal conductance model (Medlyn et al., 2011), the key biotic parameter V_{cmax25} for each day and each canopy cohort was then inversed with the model input from the measured A_n, along with leaf surface CO_2 concentration and air pressure measurements (Methods S1). The actual leaf photosynthesis rates under real-time were estimated with the in situ measured biotic (V_{cmax25}) and abiotic (air temperature, VPD, PAR, leaf surface CO_2 concentration, and air pressure) data through the coupled FvCB model and Medlyn model (Methods S1). Here, the temperature and VPD data were obtained from the nearby weather station, and the incident PAR, leaf surface CO_2 concentration, and air pressure for each leaf were recorded by LI-6400 when we measured A_n. This model was validated by measurements of A-ci curves (Methods S1, Figure S2).

Furthermore, we also estimated canopy photosynthesis (An_{canopy}) by multiple layer model which combined canopy radiation transfer model and the FvCB model of calculating photosynthesis rates of sunlit and shaded fractions (Wu, Serbin, et al., 2017) (Methods S2). We separated the whole canopy into 10 layers (n = 10), and partitioned the canopy top incident PAR (approximated by open field PAR, PAR_0) into the direct and diffuse components using an empirical model according to our in situ measurements (Methods S2, Figure S3). Then we tracked the light transfer across these 10 canopy layers. Briefly, we calculated absorbed PAR by sunlit fractions ($PAR_{sun,i}$) and by shaded fractions ($PAR_{shade,i}$), and leaf area index of sunlit fractions ($LAI_{sun,i}$) and shaded fractions ($LAI_{shade,i}$) for each layer i (i = 1, 2, …,n), respectively (Methods S2). Considering the vertical profile of leaf physiology, we also calculated leaf V_{cmax} of each canopy layer ($V_{cmax,i}$) assuming that V_{cmax25} declines exponentially within the canopy (Methods S2) (Lloyd et al., 2010; Wu, Serbin, et al., 2017). Next, we calculated photosynthesis rates for sunlit fractions ($An_{sun,i}$) and shaded fractions ($An_{shade,i}$) for each canopy layer i, based on $PAR_{sun,i}$, $PAR_{shade,i}$, $V_{cmax,i}$, and other ambient environmental conditions (i.e., air temperature and VPD). Finally, the whole canopy photosynthesis was estimated by the following equation:

$$An_{canopy} = \sum_{i=1}^{n} (An_{sun,i} \times LAI_{sun,i} + An_{shade,i} \times LAI_{shade,i}) \quad (1)$$

The annual LAI (m^2/m^2) of 2012 and 2013 was 2.69 and 3.48, respectively, and was obtained by multiplying the dry weight of leaf litter (g/m^2) by the specific leaf area (m^2/g).

2.5 | Statistical analysis

Linear regressions and Pearson correlations were used to analyze the relationships between environmental variables (aerosol loading and meteorological variables) and plant physiology (leaf photosynthesis rates and daily stem growth). Structural equation modeling (*SEM*) was used to statistically explore the mechanistic pathways between the multiple correlated environmental and plant physiological variables and to quantify the relative effect of these environmental variables on plant physiological response (Methods S3) (Grace, 2006).

3 | RESULTS

3.1 | Changes in meteorological variables under different aerosol loading

The AOD range in our study was from 0.1 to 1.9 (Figure 1). The increase in aerosol loading was accompanied with significant changes in metrological conditions. Total solar radiation and direct radiation were significantly negatively correlated with AOD, while diffuse radiation was positively correlated with AOD (Figure 1a, b and Figure S4). Therefore, the fraction of diffuse radiation showed a strong positive correlation with AOD (Figure S4). Both air temperature and vapor pressure deficit (VPD) decreased significantly with AOD (Figure 1c, d, and Figure S5).

3.2 | Responses of tree stem growth and the diving factors

Our field observations demonstrated that the daily stem growth (mm^2 day^{-1}) of aspen during growing season exhibited significant day-to-day variation (Figure 2a). The detrended daily stem growth increased linearly by 1.5 mm^2 day^{-1} (3.11% of mean daily growth) for every 0.1 increase in the detrended daily mean AOD (Figure 2b) and decreased linearly by 1.7 mm^2 day^{-1} (3.52% of mean daily growth) for every 0.1 kPa increase in the detrended daily mean VPD (Figure 2c).

Structural equation modeling (*SEM*) analysis was further conducted to assess the relative contribution of changes in radiation regime and VPD on stem growth. The *SEM* suggested that daily stem growth was stimulated by the increased fraction of diffuse solar radiation, but was not affected by total radiation (Figure 3a). Vapor pressure deficit (VPD), which was negatively correlated with AOD, had a strong negative impact on growth (Figure 3a, $p < 0.001$). Standardized total effects showed that the enhanced plant growth was mainly driven by the increase in AOD and the decrease in VPD (Figure 3b), and the absolute magnitude of the standardized total effect of VPD (−0.28) was 58% of the effect of AOD (0.48).

3.3 | Responses of leaf photosynthesis and the driving factors

To explore the physiological mechanisms underlying the response of tree stem growth to aerosols, we estimated the actual leaf photosynthesis rates based on a mechanistic leaf photosynthesis model, which was simultaneously driven by field biotic and abiotic observations during growing seasons of 2012 and 2013 (see details in Material and Methods and Methods S1). The results showed that photosynthesis rates of both sun and shade leaves had significantly positive relationships with AOD (Figure 4a and b, both $p < 0.01$). For every 0.1 increase in AOD, photosynthetic rates of sun and shade leaves increased by 0.14 and 0.33 μmol CO_2 m^{-2} s^{-1}, equivalent to 0.56% and 10.71% of their mean photosynthesis, respectively. Furthermore, the photosynthesis of the entire canopy, estimated with a multilayer canopy model (Figure 4c and Methods S2), also increased linearly with increased AOD.

The mechanistic pathways between the multiple correlated environmental variables and leaf photosynthesis were explored by *SEM*. For sun leaves, *SEM* showed that photosynthesis was negatively correlated with VPD, but was not significantly correlated with PAR_o (which represented PAR received by sun leaves) or air temperature (Figure 5a). The increasing photosynthesis of sun leaves with aerosol mainly was driven by the decreasing VPD that associated with increasing AOD, as the standardized total effects of aerosol on photosynthesis of sun leaves (−0.11) were only 18% of the effects of VPD (−0.60, Figure 5c).

For shade leaves, photosynthesis showed a highly positive correlation with PAR_i (which represented PAR received by shade leaves, Figure 5b). Aerosols enhanced photosynthesis mainly through increasing PAR_i (Figure 5b, d). The standardized total effects showed that photosynthesis of shade leaves was predominantly driven by the positive effects of AOD on PAR_i (0.71, Figure 5d), whereas both air temperature (−0.06) and VPD (−0.04) had little effects (Figure 5d).

4 | DISCUSSION

Although the effects of aerosols on ecosystem carbon exchanges have long been studied, few advances have been made in the response of tree growth and the underlying physiological processes. In this study, we monitored the responses of daily stem growth and leaf photosynthesis under an exceptionally wide range of aerosol loadings from 0.1 to 1.9, which was much wider than the reported values from most previous studies (Doughty et al., 2010, Kanniah, Beringer, Tapper, & Long, 2010, Niyogi et al., 2004), and comparable to episodic haze events induced by biomass burning in the Amazon (Cirino et al., 2014; Oliveira et al., 2007; Yamasoe et al., 2006). We also partitioned the relative influence of aerosols and the accompanying meteorological conditions on plant responses.

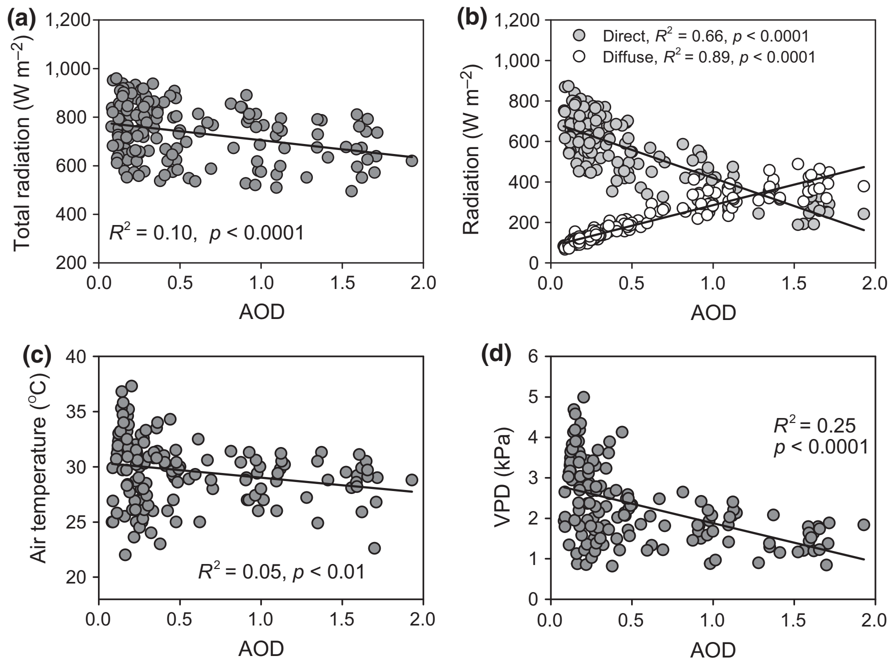

FIGURE 1 Meteorological conditions under different aerosol optical depth (AOD). (a) Total solar radiation, (b) direct and diffuse radiation, (c) air temperature, and (d) vapor pressure deficit (VPD) under different AOD. All observations were measured between 9:00 and 11:00 a.m. in 2014 and 2015 growing seasons

Although previous studies showed that ecosystem net carbon uptake was promoted by the diffuse radiation fertilization effect (Gu et al., 2002; Hollinger et al., 1994; Mercado et al., 2009), it remains uncertain whether tree growth can also benefit from a higher aerosol-laden sky (Krakauer & Randerson, 2003). In our study, we found that tree stem growth rates were enhanced significantly during high aerosol loading days (Figure 2b). Further *SEM* results indicated that the increased stem growth can be attributed to the higher fraction of diffuse solar radiation and the lower vapor pressure deficit (VPD). Tree radial stem growth consists of two parts: new structural tissue formation which is associated with photosynthesis and the cell expansion which is mainly driven by turgor changes associated with plant water potential (Steppe, Sterck, & Deslauriers, 2015). The positive response of stem growth rates to increase in diffuse radiation revealed by the *SEM* analysis was consistent with the higher photosynthesis induced by aerosols' diffuse radiation fertilization effect in the current study (discussed as below) and also previous studies (Cirino et al., 2014; Cohan et al., 2002; Gu et al., 2003; Knohl & Baldocchi, 2008). Several recent studies also revealed that stem growth is controlled by water potential aside from carbon supply (Delpierre, Berveiller, Granda, & Dufrêne, 2016; Lempereur et al., 2015). Under aerosol-laden conditions, the accompanying lower VPD could reduce canopy transpiration (Greenwald et al., 2006) and thus contribute to the maintenance of stem turgor pressure, which is in line with our observation that stem daytime shrinkage induced by water loss is lower under high AOD (Figure S6). The effect of VPD on stem daily growth highlighted that the covarying meteorological conditions had an important role in modulating the response of tree growth under aerosols conditions.

Furthermore, our study showed a consistent positive relationship between photosynthesis of both sun and shade leaves and aerosol loading (Figure 4), but the mechanisms underlying their responses were different. For sun leaves, the reduction in PAR induced by aerosols had limited negative impact on their photosynthesis (Figure 5a, Figures S7 and S8), whereas the concurrent low VPD significantly enhanced photosynthesis probably through increasing stomatal conductance (Figure 5a) (Moriana et al., 2002). Indeed, our structural equation modeling results showed that the total effect of VPD on photosynthesis (−0.60) was more than five times that of AOD (−0.11) for sun leaves (Figure 5c). For shade leaves, the increase in photosynthesis was mainly because diffuse light increased under higher aerosol-loading environment (Figure 1). The increase in diffuse light resulted in more light penetrating the inner canopy (Figure S7) thus stimulated the photosynthesis rate of shade leaves (Figure 5b) (Li et al., 2016; Reinhardt & Smith, 2016). Both VPD and air temperature had little effects on shade leaf photosynthesis (Figure 5b and d).

We further estimated the photosynthesis of the entire canopy with a multilayer canopy model (Figure 4c, and Methods S2). Consistent with the faster daily stem growth which presented above (Figure 2), our modeled canopy photosynthesis showed a positive linear relationship with AOD (Figure 4c). This finding is in contrast with the hump-shaped canopy photosynthesis responses to AOD reported in previous model studies (Cohan et al., 2002; Knohl & Baldocchi, 2008; Mercado et al., 2009), which found that canopy carbon uptake began to decline when AOD was higher than around 0.8 or the diffuse fraction greater than around 0.45 under aerosol-loading skies. Such decline was interpreted as that the diffuse radiation fertilization effect could not compensate the reduction in total solar radiation (Hollinger et al., 1994; Kanniah et al., 2012; Knohl & Baldocchi, 2008; Oliphant et al., 2011). However, our field measurement demonstrated that inner canopy PAR still continued to increase after AOD reached 1.5 (Figure S7), at which time the corresponding diffuse fraction was around 0.6 (Figure S4). Therefore, the light environment in shade

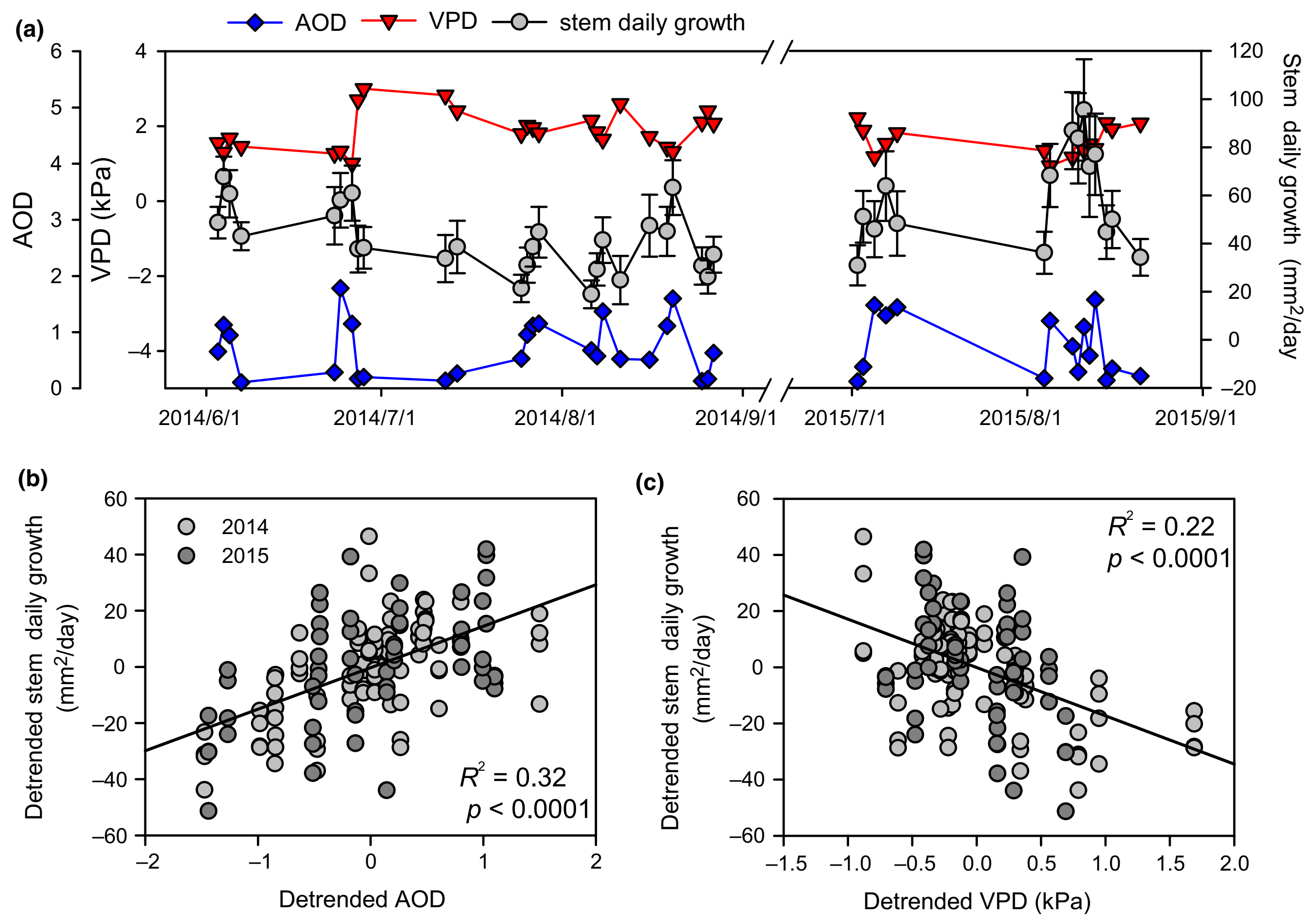

FIGURE 2 Aspen stem growth under different aerosol loading. (a) Dynamics of daily mean aerosol optical depth (AOD), vapor pressure deficit (VPD), and aspen stem daily growth (mean ± SE, n = 4) during cloud-free days in the 2014 and 2015 growing season. (b) Relationships between the detrended aspen stem daily growth and the detrended AOD. (c) Relationships between the detrended aspen stem daily growth and the detrended VPD

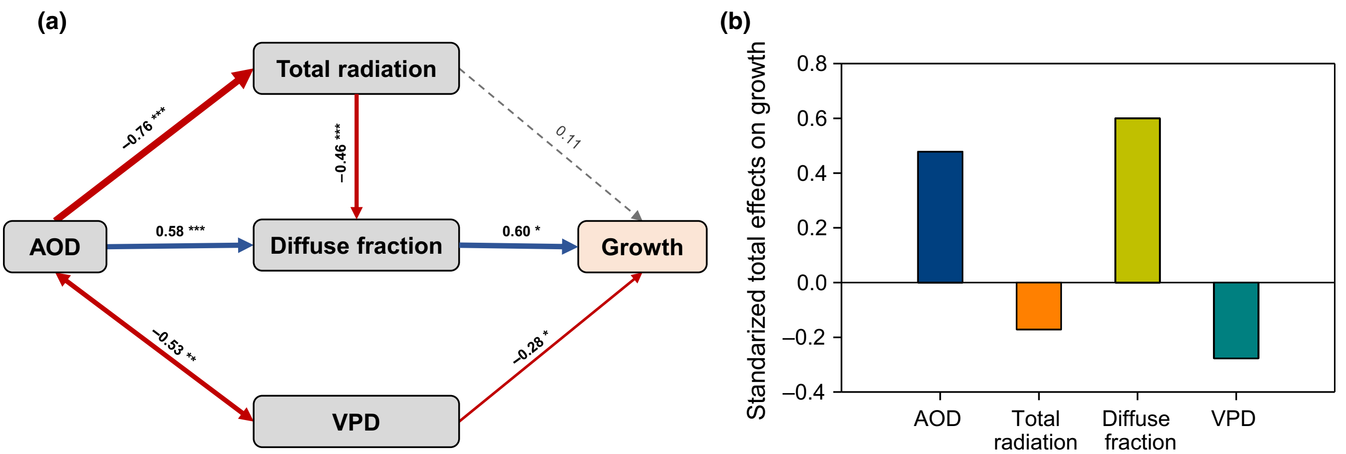

FIGURE 3 Structural equation models of the direct and indirect effects of aerosols on aspen stem growth. (a) The path coefficients for aspen stem daily growth. (b) Standardized total effects of aerosol optical depth (AOD) and meteorological factors on stem daily growth. All variables were detrended with the first-difference filter. In (a), solid arrows indicate significant relationships. Gray dash arrows indicate nonsignificant relationships ($p > 0.05$). The width of the arrows indicates the strength of the relationships. Numbers adjacent to arrows are standardized path coefficients and are indicative of the effect size of the relationship. * indicates $p < 0.05$, ** indicates $p < 0.01$, and *** indicates $p < 0.001$. The final model fits the data well, as suggested by the chi-square and RMSEA values (χ^2=0.449, p = 0.930, RMSEA < 0.001, df = 3). Variable abbreviations: AOD: aerosol optical depth; VPD: vapor pressure deficit; Growth: aspen stem daily growth

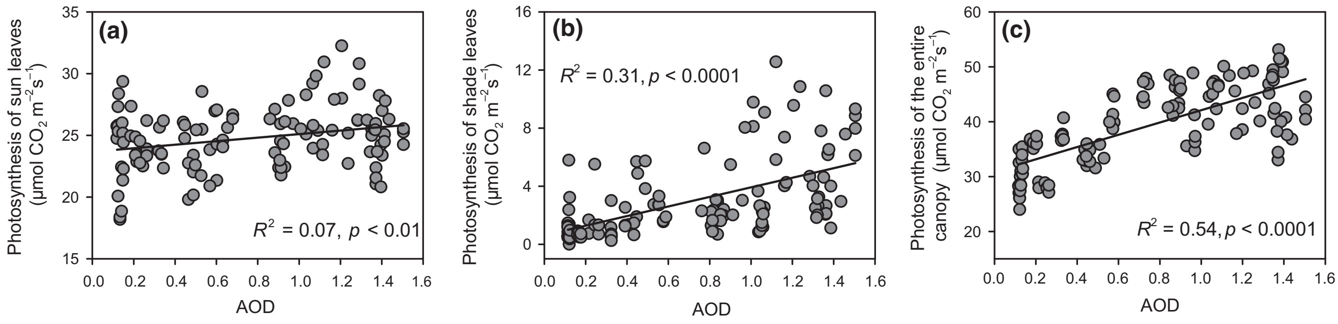

FIGURE 4 Aspen leaf and canopy photosynthesis rates under different aerosol optical depth (AOD). (a) Photosynthesis rates of sun leaves (μmol CO_2 m^{-2} s^{-1}), (b) photosynthesis rates of shade leaves (μmol CO_2 m^{-2} s^{-1}), (c) photosynthesis of the entire canopy (μmol CO_2 m^{-2} s^{-1}, the m^2 refers to ground area) under different AOD. All measurements were made in the 2012 and 2013 growing seasons

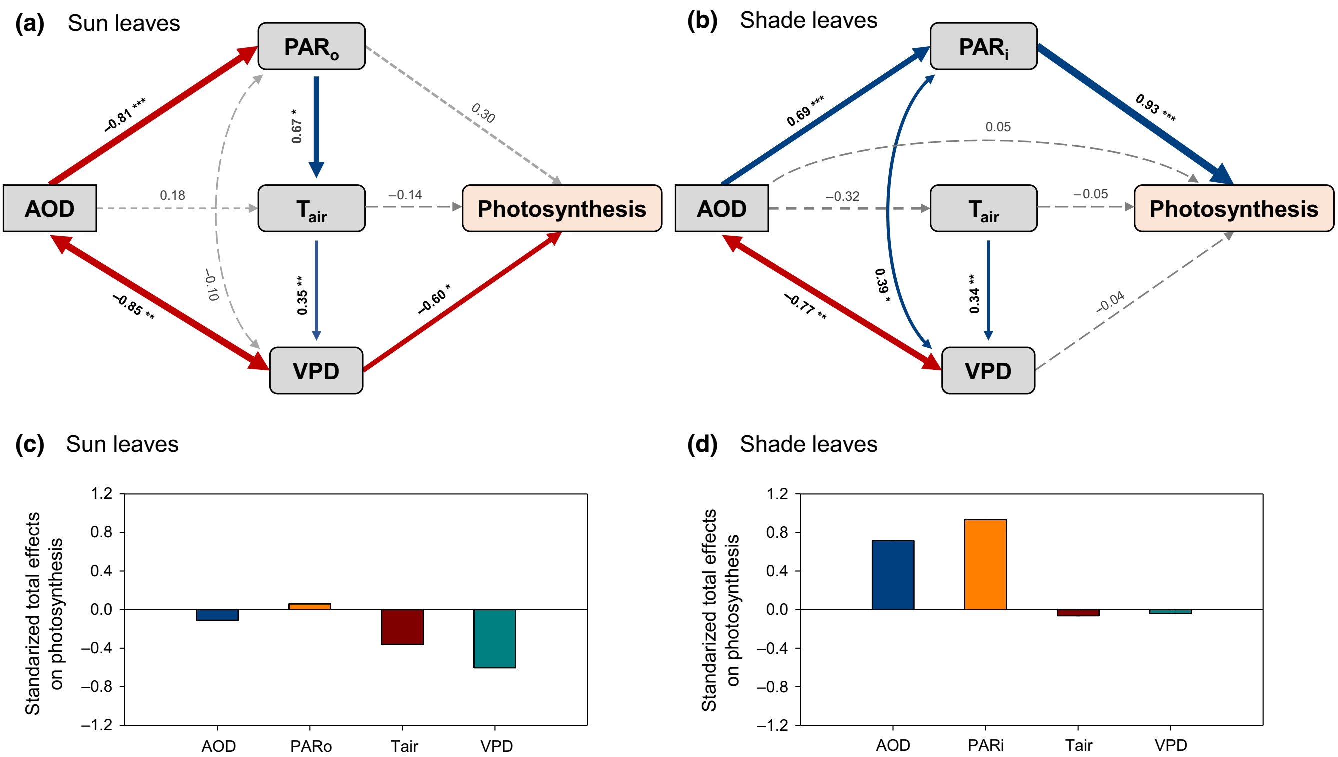

FIGURE 5 Structural equation models of the direct and indirect effects of aerosols on aspen leaf photosynthesis. (a, b) The path coefficients for aspen sun leaves and shade leaves. Solid arrows indicate significant relationships. Gray dash arrows indicate nonsignificant relationships ($p > 0.05$). The width of the arrows indicates the strength of the relationships. Numbers adjacent to arrows are standardized path coefficients and are indicative of the effect size of the relationship. * indicates $p < 0.05$, ** indicates $p < 0.01$, and *** indicates $p < 0.001$. The final models fit the data well, as suggested by the chi-square and RMSEA values (For sun leaves, $\chi^2 = 0.688$, $p = 0.407$, RMSEA < 0.001, $df = 1$; for shade leaves, $\chi^2=0.840$, $p = 0.359$, RMSEA < 0.001, $df = 1$). (c, d) Standardized total effects (derived from the structural equation models) of AOD and meteorological factors on photosynthesis of sun leaves and shade leaves. Variable abbreviations: AOD: aerosol optical depth; PAR_o: PAR received by sun leaves; PAR_i: PAR received by shade leaves; T_{air}: air temperature; VPD: vapor pressure deficit

leaves continued to improve for photosynthesis. Meanwhile, PAR received by sun leaves was still around the optimum level even under the highest aerosol loading (Figures S7 and S8).

In summary, our study provides the first field evidence on aerosol's positive effects on stem daily growth. We identified that the enhanced photosynthesis in both sun and shade-grown leaf contributes to the faster stem growth rates. We also demonstrated that the accompanying lower VPD played an important role in modulating plant responses to aerosols, and the effects of aerosol loading on leaf photosynthesis were mechanistically different for sun and shade leaves. The observed increase in stem growth indicates that aerosol pollution could increase net primary productivity. While high aerosol emitting countries, such as China, are implementing more stringent emission control to improve the air quality, the reduction in aerosol emission will likely come with a decrease in carbon benefit from aerosols, in which case an even deeper cut in carbon dioxide emission may be needed to achieve the goal of mitigating climate change. Our study also highlights that, besides the aerosol's direct radiative effect, its indirect effect on other environmental factors (e.g., especially VPD) is at least equally important. The future earth system model analysis needs to improve model structure of aerosol-meteorology interactions to better understand the impact of aerosols on ecosystem carbon cycle.

Our results provide empirical estimates of the aerosol effect that can help to benchmark earth system models. However, this is just the first step toward a better understanding aerosol's effect at leaf- and individual tree-level. Plants' sensitivities to light and VPD could be species-specific (Hanba, Kogami, & Terashima, 2002; Lambers, Chapin III, & Pons, 2008; Tardieu & Simonneau, 1998), and the physiological responses to aerosol are also influenced by their canopy structure. For example, ecosystems with simple canopy structure may gain little benefit from diffuse fertilization induced by aerosols (Matsui, Beltran-Przekurat, Niyogi, Pielke, & Coughenour, 2008, Niyogi et al., 2004, Wohlfahrt et al., 2008). More field studies on different species in different biomes are needed to assess the generality of the findings. Furthermore, at yearly or longer time scale, aerosols' overall impact on plant carbon assimilation and growth is still unclear and depends on its interaction with other biotic and meteorological factors, such as canopy structure (Niyogi et al., 2004, Wohlfahrt et al., 2008), cloud cover (Chen & Zhuang, 2014; Knohl & Baldocchi, 2008), and other coexisting air pollutants (Yue et al., 2017). The response of leaf respiration (Yue et al., 2017) to aerosol can also be important considering aerosol's cooling effect on leaf temperature (Figure S9). Understanding those ecophysiological mechanisms is critical for a better projection of the carbon-climate feedback, especially under the scenario that industrializing countries are endeavored to abate aerosol pollution.

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REFERENCES

Chen, M., & Zhuang, Q. L. (2014). Evaluating aerosol direct radiative effects on global terrestrial ecosystem carbon dynamics from 2003 to 2010. *Tellus Series B-chemical and Physical Meteorology*, *66*, 1–19. https://doi.org/10.3402/tellusb.v66.21808

Cirino, G. G., Souza, R. A. F., Adams, D. K., & Artaxo, P. (2014). The effect of atmospheric aerosol particles and clouds on net ecosystem exchange in the Amazon. *Atmospheric Chemistry and Physics*, *14*, 6523–6543. https://doi.org/10.5194/acp-14-6523-2014

Cohan, D. S., Xu, J., Greenwald, R., Bergin, M. H., & Chameides, W. L. (2002). Impact of atmospheric aerosol light scattering and absorption on terrestrial net primary productivity. *Global Biogeochemical Cycles*, *16*, 1–12. https://doi.org/10.1029/2001gb001441

Collatz, G. J., Ball, J. T., Grivet, C., & Berry, J. A. (1991). Physiological and environmental regulation of stomatal conductance, photosynthesis and transpiration: A model that includes a laminar boundary layer. *Agricultural and Forest Meteorology*, *54*, 107–136. https://doi.org/10.1016/0168-1923(91)90002-8

Delpierre, N., Berveiller, D., Granda, E., & Dufrêne, E. (2016). Wood phenology, not carbon input, controls the interannual variability of wood growth in a temperate oak forest. *New Phytologist*, *210*, 459–470. https://doi.org/10.1111/nph.13771

Doughty, C. E., Flanner, M. G., & Goulden, M. L. (2010). Effect of smoke on subcanopy shaded light, canopy temperature, and carbon dioxide uptake in an Amazon rainforest. *Global Biogeochemical Cycles*, *24*, GB3015. https://doi.org/10.1029/2009gb003670

Ebert, M., Inerle-Hof, M., & Weinbruch, S. (2002). Environmental scanning electron microscopy as a new technique to determine the hygroscopic behaviour of individual aerosol particles. *Atmospheric Environment*, *36*, 5909–5916. https://doi.org/10.1016/S1352-2310(02)00774-4

Farquhar, G. D., Von Caemmerer, S., & Berry, J. A. (1980). A biochemical model of photosynthetic CO2 assimilation in leaves of C3 species. *Planta*, *149*, 78–90. https://doi.org/10.1007/BF00386231

Grace, J. B. (2006). *Structural equation modeling and natural systems*. New York, USA: Cambridge University Press.

Greenwald, R., Bergin, M. H., Xu, J., Cohan, D., Hoogenboom, G., & Chameides, W. L. (2006). The influence of aerosols on crop production: A study using the CERES crop model. *Agricultural Systems*, *89*, 390–413. https://doi.org/10.1016/j.agsy.2005.10.004.

Gu, L. H., Baldocchi, D., Verma, S. B., Black, T. A., Vesala, T., Falge, E. M., & Dowty, P. R. (2002). Advantages of diffuse radiation for terrestrial ecosystem productivity. *Journal of Geophysical Research*, *107*, 1–23. https://doi.org/10.1029/2001dj001242

Gu, L. H., Baldocchi, D. D., Wofsy, S. C., Munger, J. W., Michalsky, J. J., Urbanski, S. P., & Boden, T. A. (2003). Response of a deciduous forest to the Mount Pinatubo eruption: Enhanced photosynthesis. *Science*, *299*, 2035–2038. https://doi.org/10.1126/science.1078366

Guo, S., Hu, M., Zamora, M. L., Peng, J., Shang, D., Zheng, J., & Zhang, R. (2014). Elucidating severe urban haze formation in China. *Proceedings of the National Academy of Sciences of the United States of America*, *111*, 17373–17378. https://doi.org/10.1073/pnas.1419604111

Hanba, Y. T., Kogami, H., & Terashima, I. (2002). The effect of growth irradiance on leaf anatomy and photosynthesis in Acer species differing in light demand. *The Plant Celland Environment*, *25*, 1021–1030. https://doi.org/10.1046/j.1365-3040.2002.00881.x

Hollinger, D., Kelliher, F., Byers, J., Hunt, J., Mcseveny, T., & Weir, P. (1994). Carbon dioxide exchange between an undisturbed old-growth temperate forest and the atmosphere. *Ecology*, *75*, 134–150. https://doi.org/10.2307/1939390

Hsu, N. C., Gautam, R., Sayer, A. M., Bettenhausen, C., Li, C., Jeong, M. J., & Holben, B. N. (2012). Global and regional trends of aerosol optical depth over land and ocean using SeaWiFS measurements from

1997 to 2010. *Atmospheric Chemistry and Physics*, *12*, 8037–8053. https://doi.org/10.5194/acp-12-8037-2012

Hussein, T., Karppinen, A., Kukkonen, J., Härkönen, J., Aalto, P. P., Hämeri, K., & Kulmala, M. (2006). Meteorological dependence of size-fractionated number concentrations of urban aerosol particles. *Atmospheric Environment*, *40*, 1427–1440. https://doi.org/10.1016/j.atmosenv.2005.10.061

IPCC (2013). *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, UK & New York, NY, USA: Cambrige University Press.

Kanniah, K. D., Beringer, J., North, P., & Hutley, L. (2012). Control of atmospheric particles on diffuse radiation and terrestrial plant productivity: A review. *Progress in Physical Geography*, *36*, 209–237. https://doi.org/10.1177/0309133311434244

Kanniah, K. D., Beringer, J., Tapper, N. J., & Long, C. N. (2010). Aerosols and their influence on radiation partitioning and savanna productivity in northern Australia. *Theoretical and Applied Climatology*, *100*, 423–438. https://doi.org/10.1007/s00704-009-0192-z

Knohl, A., & Baldocchi, D. D. (2008). Effects of diffuse radiation on canopy gas exchange processes in a forest ecosystem. *Journal of Geophysical Research*, *113*, 1–17. https://doi.org/10.1029/2007jg000663

Krakauer, N. Y., & Randerson, J. T. (2003). Do volcanic eruptions enhance or diminish net primary production? Evidence from tree rings. *Global Biogeochemical Cycles*, *17*, 1–12. https://doi.org/10.1029/2003gb002076

Lambers, H., Chapin Iii, F. S., & Pons, T. L. (2008). *Plant Physiological Ecology*. New York, USA: Springer.

Lempereur, M., Martin-Stpaul, N. K., Damesin, C., Joffre, R., Ourcival, J. M., Rocheteau, A., & Rambal, S. (2015). Growth duration is a better predictor of stem increment than carbon supply in a Mediterranean oak forest: Implications for assessing forest productivity under climate change. *New Phytologist*, *207*, 579–590. https://doi.org/10.1111/nph.13400.

Li, T., Kromdijk, J., Heuvelink, E., Van Noort, F. R., Kaiser, E., & Marcelis, L. F. M. (2016). Effects of Diffuse Light on Radiation Use Efficiency of Two Anthurium Cultivars Depend on the Response of Stomatal Conductance to Dynamic Light Intensity. *Frontiers in Plant Science*, *7*, 1–10. https://doi.org/10.3389/fpls.2016.00056

Lloyd, J., Patino, S., Paiva, R. Q., Nardoto, G. B., Quesada, C. A., Santos, A. J. B., … Mercado, L. M. (2010). Optimisation of photosynthetic carbon gain and within-canopy gradients of associated foliar traits for Amazon forest trees. *Biogeosciences*, *7*, 1833–1859. https://doi.org/10.5194/bg-7-1833-2010

Mahowald, N., Ward, D. S., Kloster, S., Flanner, M. G., Heald, C. L., Heavens, N. G., & Chuang, P. Y. (2011). Aerosol impacts on climate and biogeochemistry. *Annual Review of Environment and Resources*, *36*, 45–74. https://doi.org/10.1146/annurev-environ-042009-094507

Mann, M. E., Fuentes, J. D., & Rutherford, S. (2012). Underestimation of volcanic cooling in tree-ring-based reconstructions of hemispheric temperatures. *Nature Geoscience*, *5*, 202–205. https://doi.org/10.1038/ngeo1394

Matsui, T., Beltran-Przekurat, A., Niyogi, D., Pielke, R. A. Sr, & Coughenour, M. (2008). Aerosol light scattering effect on terrestrial plant productivity and energy fluxes over the eastern United States. *Journal of Geophysical Research-Atmospheres*, *113*, D14S14. https://doi.org/10.1029/2007jd009658

Medlyn, B. E., Duursma, R. A., Eamus, D., Ellsworth, D. S., Prentice, I. C., Barton, C. V. M., & Wingate, L. (2011). Reconciling the optimal and empirical approaches to modelling stomatal conductance. *Global Change Biology*, *17*, 2134–2144. https://doi.org/10.1111/j.1365-2486.2010.02375.x

Mercado, L. M., Bellouin, N., Sitch, S., Boucher, O., Huntingford, C., Wild, M., & Cox, P. M. (2009). Impact of changes in diffuse radiation on the global land carbon sink. *Nature*, *458*, 1014–1017. https://doi.org/10.1038/nature07949

Moriana, A., Villalobos, F. J., & Fereres, E. (2002). Stomatal and photosynthetic responses of olive (Olea europaea L.) leaves to water deficits. *The Plant Celland Environment*, *25*, 395–405. https://doi.org/10.1046/j.0016-8025.2001.00822.x

Niyogi, D., Chang, H. I., Saxena, V. K., Holt, T., Alapaty, K., Booker, F., & Xue, Y. K. (2004). Direct observations of the effects of aerosol loading on net ecosystem CO2 exchanges over different landscapes. *Geophysical Research Letters*, *31*, 1–5. https://doi.org/10.1029/2004gl020915

Oliphant, A. J., Dragoni, D., Deng, B., Grimmond, C. S. B., Schmid, H. P., & Scott, S. L. (2011). The role of sky conditions on gross primary production in a mixed deciduous forest. *Agricultural and Forest Meteorology*, *151*, 781–791. https://doi.org/10.1016/j.agrformet.2011.01.005

Oliveira, P. H. F., Artaxo, P., Pires, C., De Lucca, S., Procopio, A., Holben, B., & Rocha, H. R. (2007). The effects of biomass burning aerosols and clouds on the CO2 flux in Amazonia. *Tellus Series B-chemical and Physical Meteorology*, *59*, 338–349. https://doi.org/10.1111/j.1600-0889.2007.00270.x

Reinhardt, K., & Smith, W. K. (2016). Chlorophyll fluorescence and photosynthetic gas exchange under direct versus diffuse light in evergreen conifer (*Picea pungens*) shoots and broadleaf shrub (*Rhododendron ponticum*) leaves. *Plant Ecology*, *217*, 443–450. https://doi.org/10.1007/s11258-016-0586-9

Rocha, A. V., Goulden, M. L., Dunn, A. L., & Wofsy, S. C. (2006). On linking interannual tree ring variability with observations of whole-forest CO2 flux. *Global Change Biology*, *12*, 1378–1389. https://doi.org/10.1111/j.1365-2486.2006.01179.x

Roderick, M. L., Farquhar, G. D., Berry, S. L., & Noble, I. R. (2001). On the direct effect of clouds and atmospheric particles on the productivity and structure of vegetation. *Oecologia*, *129*, 21–30. https://doi.org/10.1007/s004420100760

Smirnov, A., Holben, B. N., Eck, T. F., Dubovik, O., & Slutsker, I. (2000). Cloud-Screening and Quality Control Algorithms for the AERONET Database. *Remote Sensing of Environment*, *73*, 337–349. https://doi.org/10.1016/S0034-4257(00)00109-7

Steiner, A. L., & Chameides, W. L. (2005). Aerosol-induced thermal effects increase modelled terrestrial photosynthesis and transpiration. *Tellus Series B-chemical and Physical Meteorology*, *57*, 404–411. https://doi.org/10.3402/tellusb.v57i5.16559

Steppe, K., Sterck, F., & Deslauriers, A. (2015). Diel growth dynamics in tree stems: Linking anatomy and ecophysiology. *Trends in Plant Science*, *20*, 335–343. https://doi.org/10.1016/j.tplants.2015.03.015

Tardieu, F., & Simonneau, T. (1998). Variability among species of stomatal control under fluctuating soil water status and evaporative demand: Modelling isohydric and anisohydric behaviours. *Journal of Experimental Botany*, *49*, 419–432. https://doi.org/10.1093/jexbot/49.suppl_1.419

Wohlfahrt, G., Hammerle, A., Haslwanter, A., Bahn, M., Tappeiner, U., & Cernusca, A. (2008). Disentangling leaf area and environmental effects on the response of the net ecosystem CO2 exchange to diffuse radiation. *Geophysical Research Letters*, *35*, L16805. https://doi.org/10.1029/2008gl035090

Wu, J., Guan, K., Hayek, M., Restrepo-Coupe, N., Wiedemann, K. T., Xu, X., & Da Silva, R. (2017). Partitioning controls on Amazon forest photosynthesis between environmental and biotic factors at hourly to inter-annual time scales. *Global Change Biology*, *23*, 1240–1257. https://doi.org/10.1111/gcb.13509

Wu, J., Serbin, S. P., Xu, X., Albert, L. P., Chen, M., Meng, R., & Rogers, A. (2017). The phenology of leaf quality and its within-canopy variation are essential for accurate modeling of photosynthesis in tropical evergreen forests. *Global Change Biology*, *23*, 4814–4827. https://doi.org/10.1111/gcb.13725

Yamasoe, M. A., Von Randow, C., Manzi, A. O., Schafer, J. S., Eck, T. F., & Holben, B. N. (2006). Effect of smoke and clouds on the transmissivity of photosynthetically active radiation inside the canopy. *Atmospheric Chemistry and Physics*, *6*, 1645–1656. https://doi.org/10.5194/acp-6-1645-2006

Yoon, J., Burrows, J. P., Vountas, M., Von Hoyningen-Huene, W., Chang, D. Y., Richter, A., & Hilboll, A. (2014). Changes in atmospheric aerosol loading retrieved from space-based measurements during the past decade. *Atmospheric Chemistry and Physics*, *14*, 6881–6902. https://doi.org/10.5194/acp-14-6881-2014

Yue, X., Unger, N., Harper, K., Xia, X., Liao, H., Zhu, T., & Li, J. (2017). Ozone and haze pollution weakens net primary productivity in China. *Atmospheric Chemistry and Physics*, *17*, 6073–6089. https://doi.org/10.5194/acp-17-6073-2017

SUPPORTING INFORMATION

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Graphical Abstract

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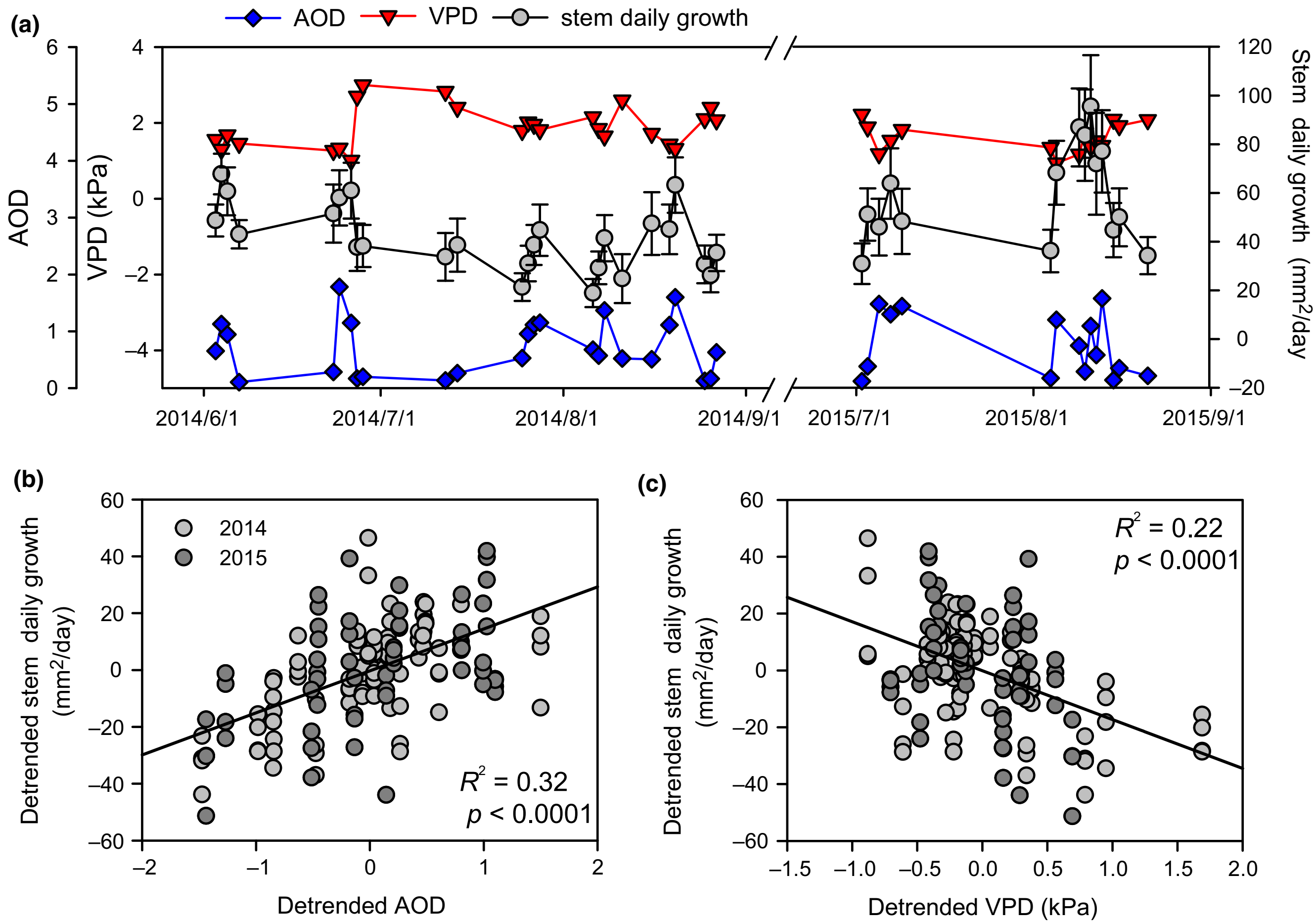

Aerosols could significantly alter terrestrial carbon uptake, but field evidence for the aerosol effect on tree growth is limited. Our study provides the first observational evidence of aerosol's positive effects on tree stem growth based on in-situ measurements. The increased stem growth can be attributed to higher canopy photosynthesis induced by diffuse radiation fertilization effect and the accompanying lower vapor pressure deficit. Our study points out that the co-varying meteorological conditions have an important role in modulating plant carbon assimilation under aerosols conditions, and highlights the importance of incorporating these mechanisms into earth system models for better simulating large-scale climate-vegetation interactions.