THESIS

DOSE-DEPENDENT SUPPRESSION OF LEAF-LEVEL GAS EXCHANGE BY WILDFIRE SMOKE IN CORN

Submitted by

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ABSTRACT

DOSE-DEPENDENT SUPPRESSION OF LEAF-LEVEL GAS EXCHANGE BY WILDFIRE SMOKE IN CORN

Wildfire events are increasing in frequency and intensity across many regions, raising concern about the effects of smoke on agricultural productivity and ecosystem function. Wildfire smoke contains a complex mixture of particulate matter and gases that can interact with plant leaves and potentially alter photosynthesis and plant gas exchange. However, the mechanisms by which smoke exposure influences plant physiological processes remain poorly understood. We investigated the effects of wildfire smoke particulate matter ($PM_{2.5}$) on leaf-level gas exchange in corn (*Zea mays L.*) using controlled chamber fumigation experiments. Plants were exposed to clean air or smoke for four hours at three $PM_{2.5}$ concentration ranges (400-600, 600-1000, and 1200-2000 $\mu g\ m^{-3}$). Net CO_2 assimilation and stomatal conductance were measured before and after exposures and treatment responses were evaluated using net smoke effects and relative percent changes in gas exchange compared between $PM_{2.5}$ groups. Relative percent change showed a significant ($p=0.005$) decline in net CO_2 assimilation in medium (-36%) and high (-30%) $PM_{2.5}$ concentrations when compared to control (-12%). Stomatal conductance showed no significant decrease. Interestingly, averaged values for net smoke effect showed a decreasing trend for net CO_2 assimilation with increasing $PM_{2.5}$ concentrations and the opposite trend with stomatal conductance. This observed divergence suggests reduced mesophyll conductance and biochemical impairment by two primary non-stomatal pathways, VOC-driven biochemical and diffusion constraints, and $PM_{2.5}$-driven internal and chemical effects.

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1. Introduction

Severe wildfire events have become more common over the last several decades and are predicted to increase in both frequency and intensity, with nearly two-thirds of this increase concentrated in forests of the Northern U.S. Rocky Mountains.[1–3] While wildfires are a natural and essential component of many terrestrial ecosystems,[4] they are major sources of atmospheric pollution[3–5] and raise concerns about negative impacts on ecosystem function and agricultural productivity.[6] Smoke released during wildfire events can transport hazardous particles and gases thousands of kilometers, impacting human health, air quality, and climate at local, regional, and global scales.[4,5,7] As agricultural regions are increasingly exposed to wildfire smoke, concern has grown that smoke negatively affects plant health.[3,6,8]

Smoke from wildfires is a complex mixture of both particulate matter (PM) and gaseous pollutants including carbon monoxide (CO), nitrogen oxides (NO_x), and volatile organic compounds (VOCs).[5,9,10] As smoke transports in the atmosphere, chemical reactions form ozone (O_3) and secondary particulate matter.[7,11–14] Ozone has well-established negative effects on plant physiology and crop yield,[15,16] but particulate matter is less well understood.[17,18] Several studies have shown negative impacts of PM on plant health. However, smoke also promotes germination of seeds of some plants,[19–21] while PM alters the quantity and quality of incoming light.[22] Smoke can increase diffuse radiation and thereby enhance crop productivity by increasing photosynthesis

in shaded leaves, although this effect is typically associated with smoke layers higher in the atmosphere rather than ground-level smoke.[23]

Smoke introduces chemical and physical stressors that may directly influence plant physiological processes. Smoke exposure can suppress photosynthetic rates despite elevated atmospheric CO_2 during fire events.[24] Gilbert and Ripley[25] reported substantial reductions in CO_2 assimilation and stomatal conductance in *Chrysanthemoides monilifera* following brief 1-minute smoke exposure, with evidence of both stomatal and mesophyll limitations. Calder et al.[26] observed similar declines in photosynthesis and stomatal conductance across a range of deciduous and coniferous tree species, linking the suppression to both stomatal closure and biochemical impairment. Bell et al.[8] showed that grapevine leaves experienced short-term reductions in gas exchange following 20-minute smoke exposure, with partial recovery after several hours. More recently, field observations by Riches et al.[27] confirmed near-complete stomatal closure in ponderosa pines during prolonged wildfire smoke events. Together, these laboratory and field studies emphasize the potential for wildfire smoke exposure to suppress crop and ecosystem productivity.

Due to their high surface area, plant canopies serve as major sinks for both particulate matter and gaseous pollutants.[28] Dry deposition transfers particles onto plant surfaces,[29] where they contact with leaves and potentially alter physiological functions.

The mechanism for smoke-induced suppression of plant photosynthesis is poorly understood, requiring either closure or blocking of stomates, which regulate the diffusion of CO_2, water vapor, and oxygen between the leaf interior and the atmosphere.[30,31] Three possible mechanisms thus include (i) clogging of stomata by particulate matter; (ii) stomatal closure in response to pollutants or environmental stressors; and (iii) stomata structural damage. With regards

to mechanism (i), smoke PM is dominated by particles with diameters smaller than 2.5 µm ($PM_{2.5}$). In contrast, stomatal pores in *Zea mays* (maize) are typically ~43 µm in length and ~12 µm in width and occur on leaves at densities of approximately 108 stomata mm^{-2} on the lower epidermis and 98 stomata mm^{-2} on the upper epidermis,[31] making them substantially larger than individual $PM_{2.5}$ particles. Thus, individual particles are unlikely to clog stomata, but large numbers of coagulating particles on leaf surfaces could. Recent high-resolution imaging studies showed that $PM_{2.5}$ can accumulate directly inside stomata and penetrate 5-14 µm into leaf tissue, suggesting a physical mechanism through which particulate matter may interfere with gas exchange.[32] Particle uptake is also observed when leaves are sprayed by $CaCO_3$,[33] and when 'green wall' plants were exposed to hybrid diesel fuel smoke.[34] In addition to PM, leaves also sorb gaseous substances such as trace air pollutants and VOCs. Riches et al.[27] found clear evidence for partitioning of smoke VOCs inside stomatal pores, but not evidence that these VOCs clogged pores. That said, organic molecules like abscisic acid are known to induce stomatal closure, and it is possible that plants respond to the smoke VOCs by stomatal closure via mechanism (ii). Multiple studies across a variety of species support these proposed mechanisms. While studies haven't yet investigated stomatal injury from smoke (mechanism iii), ozone and SO_2 do injure guard cells.[35–37]

Particulate matter is a mixture of solid particles and liquid droplets suspended in the air, ranging from visible dust and soot to microscopic particles detectable only with specialized instrumentation.[38,39] $PM_{2.5}$ particles are sufficiently small to remain airborne for extended periods and are widely recognized as posing the greatest risk to human health due to their ability to penetrate deep into the lungs and alveolar regions, and in some cases enter the bloodstream.[40–42]

$PM_{2.5}$ particles exhibit substantial chemical and physical diversity. They originate both from direct emissions, such as wildfires and vehicles, and from secondary atmospheric reactions

involving precursor gases including sulfur dioxide and nitrogen oxides.[30,43] These particles vary widely in size, shape, and composition and can include hundreds of different chemical species.[44] Monitoring $PM_{2.5}$ concentrations relies on both Federal Reference Methods and increasingly on low-cost optical particle counters, such as PurpleAir sensors, which infer particle concentrations by measuring laser light scattered by airborne particles.[38] According to the California Air Resources Board, optical particle counters estimate particle number and size based on the intensity of scattered light, providing a practical tool for characterizing spatial and temporal variability in particulate pollution.[38]

There is a clear need to improve our understanding of crop physiological responses to smoke under realistic conditions. While smoke can be beneficial to plants through seed germination and enhancements of diffuse radiation, ground-level smoke can clearly have negative impacts on CO_2 assimilation and thus plant growth. Field measurements are challenging to plan and safely conduct. Instead, here we use plant chambers to fumigate corn plants with leaf smoke to see impacts on leaf-level CO_2 assimilation and stomatal conductance at different smoke levels.

2. Methods

We studied smoke effects on *Zea mays L.* plants (Bicolor variety). Plants were purchased at the V7–V10 growth stage, characterized by the number of collars present on the plant, but had reached the R1 reproductive stage with visible silks by the fumigation experiment.[45] We placed plants in chambers to expose them to clean air (Control Chamber) or smoke ('Fumigation Chamber') for four hours. Physiological parameters were measured the day before experiments, before and after each chamber exposure, and the day after the fumigation experiment. With both control and fumigation experiments plus associated measurements, each full exposure experiment took four days (Figure 1a).

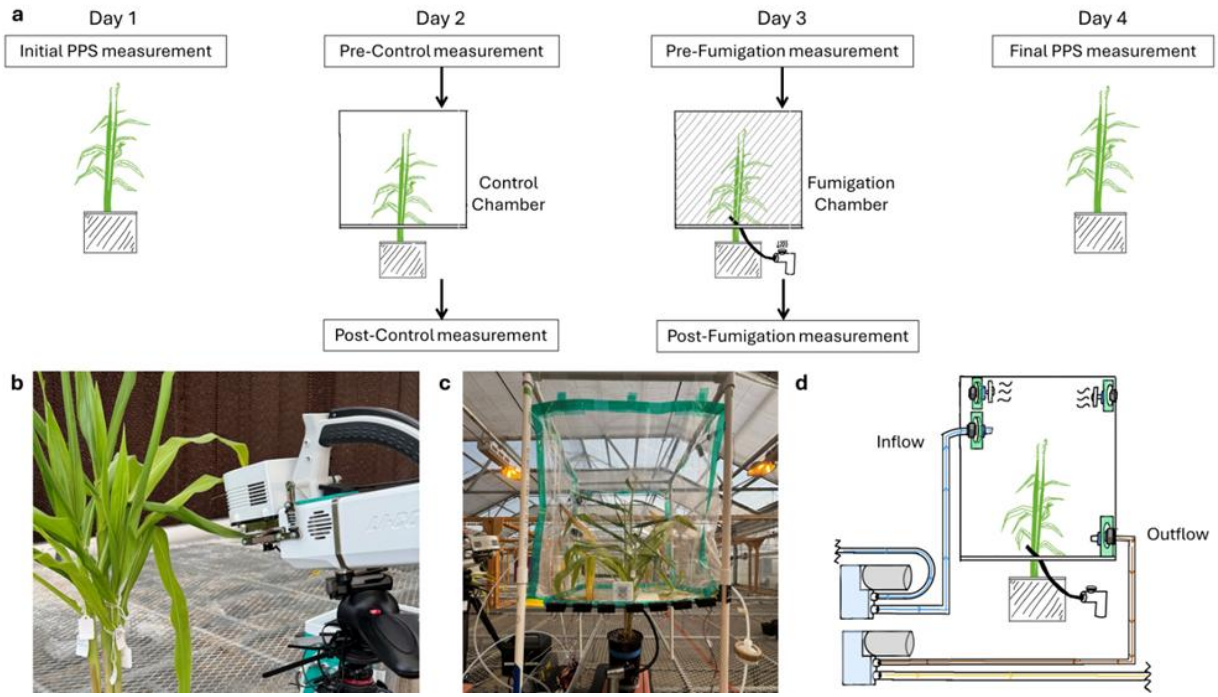

Figure 1. (a) Timeline for control and $PM_{2.5}$ fumigation treatments. (b) The Portable Photosynthesis System (PPS) measured corn CO_2 assimilation and stomatal conductance. (c) The plant chamber during a control experiment. (d) Chamber schematic showing the air exchange with inflow and outflow. Fresh smoke entered through the bottom of the chamber, while two fans on top continuously circulated chamber air.

We refer to Day 1 leaf measurements as "Initial", Day 2 as "Pre-Control" or "Post-Control", Day 3 as "Pre-Fumigation" or "Post-Fumigation", and Day 4 as "Final". We used eight pots, each containing two to three individual plants. Pots were assigned to one of three smoke exposure groups, as determined by average observed $PM_{2.5}$ being low (400-600 µg m^{-3}), medium (600-1000 µg m^{-3}), and high (1200-2000 µg m^{-3}). All experiments took place in the Colorado State University Plant Growth Facility.

We built custom 57 × 57 × 57 cm chambers of polytetrafluoroethylene (PTFE) film that are held in place with polyvinyl chloride (PVC) framing (Figure 1c). Pots were inserted up to the first leaf sheath through a 3-cm circular opening at the base. Airflow into and out of the chamber was supplied via 0.25-inch flexible tubing attached to external pumps (Hargraves C183-22-01, 7

L/min), while two fans (Orion Fans, OD4010-12HSS) continuously circulated internal chamber air (Figure 1d). An AC/DC converter (ALITOV ALT-1215T) powered the pumps and fans.

Wildfire smoke proxy was generated using a cocktail smoker (Breville BSM600) loaded with dried ponderosa pine needles (*Pinus ponderosa*) collected from the Colorado State University campus; smoke entered through the base opening of the chamber (Figure 1d). This smoke generation system, described in detail by Li et al.,[46] produces wildfire smoke with both VOC emissions and particle composition and size distributions that are representative of real, observed wildfire smoke. Average $PM_{2.5}$ was 616 ± 97 for the low exposure plants, 957 ± 97 for medium, and 1724 ± 67 µg m^{-3} for high.

CO_2 concentration, temperature, and relative humidity were continuously measured in the chamber using an Aranet4 HOME sensor. $PM_{2.5}$ concentrations were monitored using a PurpleAir PA-II optical particle counter equipped with dual PMS-5003 laser detectors, which measure particle counts across sizes ranging from 0.3 to 10 µm. No corrections were applied to the particle counting data. During both control and fumigation experiments, the chamber relative humidity was 55 ± 5% and 500 ± 50 ppm CO_2. During control exposures, $PM_{2.5}$ concentrations were 0 ± 5 µg m^{-3}. During fumigation exposures, $PM_{2.5}$ concentrations were maintained within the low, medium, and high target ranges, with initial concentrations on the upper end of those ranges and levels supplemented by additional smoke additions.

Leaf-level net CO_2 assimilation (A) and stomatal conductance (g_s) were quantified using a LI-6800 Portable Photosynthesis System (LI-COR Biosciences), which uses dual infrared gas analyzers to detect CO_2 and H_2O concentrations. When assimilation stabilized within ±0.1 µmol m^{-2} s^{-1}, we averaged data over two minutes for each leaf (Figure 2). The average value for each

plant was then taken as the average of three leaves. PPS measurements for pre-chamber were conducted between 11am-12pm on average.

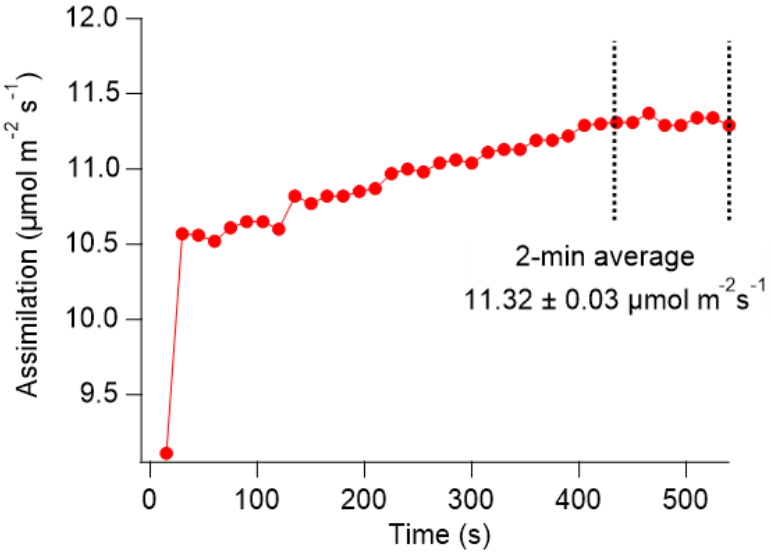

Figure 2. Example of CO2 assimilation data collected from a single leaf during a pre-exposure; assimilation values typically increased for about six minutes before reaching a steady value; we report 2-minute averages and standard deviations after assimilation rates stabilized.

To compare responses across treatments, we calculated the change in A (ΔA) and g_s (Δg_s) for each plant as the difference between post-exposure and pre-exposure chamber measurements. For example,

$$\Delta A = A_{Post} - A_{Pre}$$

$$\Delta g_s = g_{s,Post} - g_{s,Pre}$$

To isolate the effect of smoke exposure on assimilation, we subtracted the control chamber ($\Delta A_{control}$, $\Delta g_{s,control}$) from the fumigation chamber ($\Delta A_{fumigation}$, $\Delta g_{s,fumigation}$) for a given plant to determine a plant-level smoke effect:

$$Net\ Smoke\ Effect_i = \Delta_{Fumigation,i} - \Delta_{Control,i}$$

We also calculated the relative percent change for each plant's raw A (µmol m^{-2} s^{-1}) and g_s (mol m^{-2} s^{-1}) from its pre- and post- control and fumigation exposure values:

$$Relative\ Percent\ Change = \left(\frac{Value_{Post} - Value_{Pre}}{Value_{Pre}}\right) \times 100\%$$

Plant-level values were then grouped by $PM_{2.5}$ concentration and summarized as control (n=17 plants), low (n=6 plants), medium (n=4 plants), and high (n=7 plants).

3. Results

The chamber environment itself reduced net CO_2 assimilation by -12 ± 14 % (Figure 3a, 4a), but not necessarily stomatal conductance. This reduction likely reflects a chamber effect, as controlled environment chambers can introduce variability in physiological measurements such as A and g_s due to subtle differences in airflow, gas concentration, or microenvironmental conditions within the chamber environment.[47]

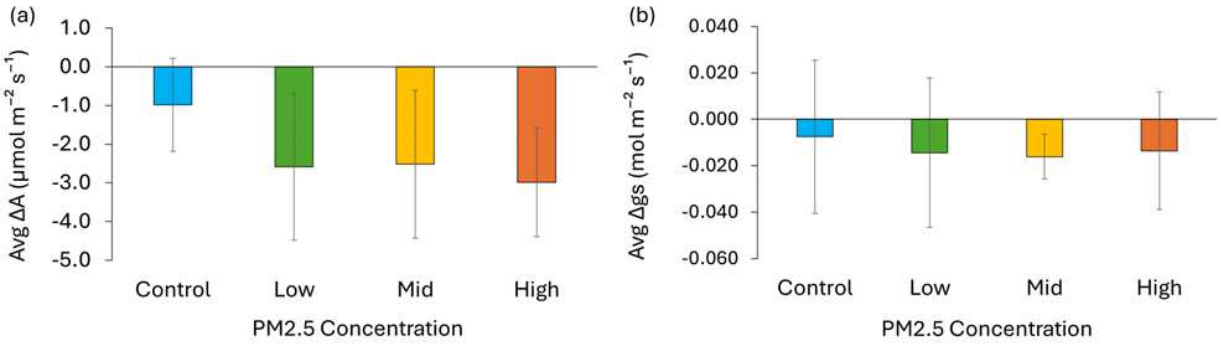

Figure 3. (a) The average ΔA and (b) Δg_s for each $PM_{2.5}$ concentration group and control (n=17). Low (n=6), Medium (n=4), High (n=7). Error bars are the standard deviation. Grubbs tests (α= 0.05) identified potential outliers in derived variables (ΔA and Δg_s) within the control group. For graphical clarity, extreme values were excluded from this figure.

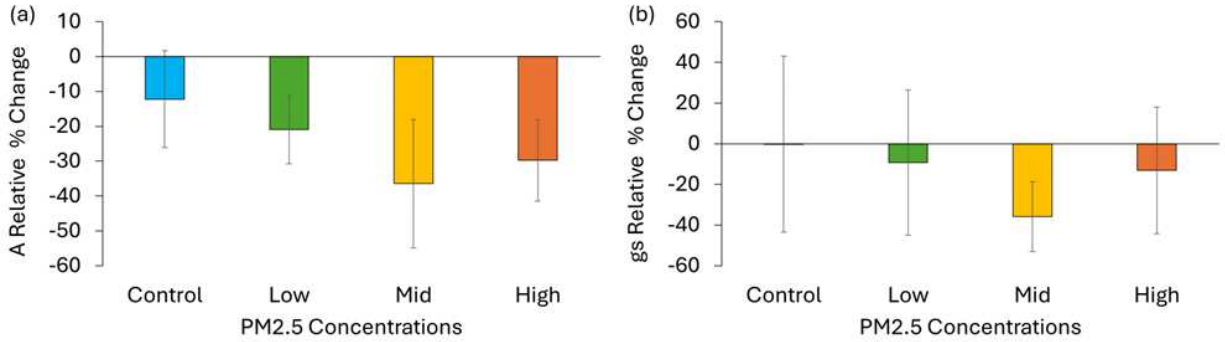

Figure 4. Relative change from pre-treatment to post-treatment for (a) Net CO_2 assimilation (A) and (b) stomatal conductance (g_s). Each plant was calculated, and percentages were averaged comparing Control (n=17), Low (n=6), Medium (n=4), High (n=7) for A and for g_s. Grubbs tests (α= 0.05) identified a potential outlier in derived variables (%g_s) within the control group. For graphical clarity, extreme values were excluded from this figure. Error bars are standard deviations.

A Grubbs test (α= 0.05) identified several potential outliers in derived variables ΔA (Figure 3a), Δg_s (Figure 3b), and g_s% (Figure 4b) within the control group. Examination of the raw gas exchange measurements indicated that these values were not associated with instrument error or abnormal chamber conditions and therefore likely reflect natural biological variability. We thus retain all observations for subsequent analysis but exclude points in noted graphs for clarity (noted in figure captions).

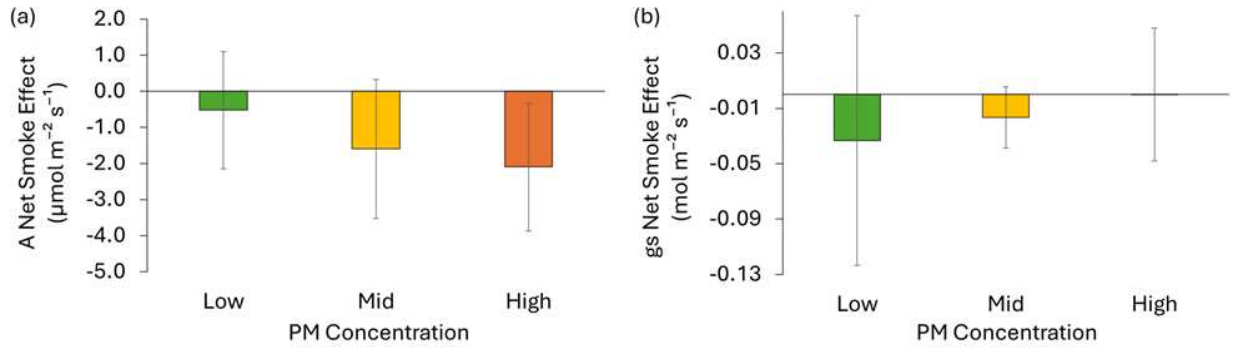

Figure 5. Net smoke effect by $PM_{2.5}$ concentration group for (a) Net CO_2 assimilation (A) and (b) stomatal conductance (g_s). Net smoke effect was calculated as the difference between fumigation and control chamber responses for each plant. Error bars are standard deviation.

Because the control response was subtracted in this calculation, net smoke effect values were compared only among the low-, mid-, and high-smoke treatments (Figure 5). One-way ANOVA showed no significant differences among treatments for net smoke effect in A ($p = 0.30$) or stomatal conductance ($p = 0.65$). Other comparisons likewise showed no significant differences between treatments (low vs medium: ΔA $t = 0.95$, Δg_s $t = 0.41$; low vs high: ΔA $t = 1.61$, Δg_s $t = 0.94$; medium vs high: ΔA $t = 0.45$, Δg_s $t = 0.42$).

Plant variability between plants was calculated to show changes between initial and chamber pre-values (Figure 6). Standard deviation was averaged for day 1 initial, day 2 pre-chamber, and day 3 pre-fumigation measurements. Plants 7-9 highlight the largest difference of all the plants, likely due to a large 8-day gap between initial and pre-control measurements because of experimental issues in the greenhouse after the first set of plant fumigation was conducted. Missing data for plants 4,5, and 11-13 were due to personal scheduling issues. Plant 15 had significant leaf yellowing and was dead the following day at the start of control treatment. A off-shoot plant that started growing later in the season was used for control and fumigation treatments.

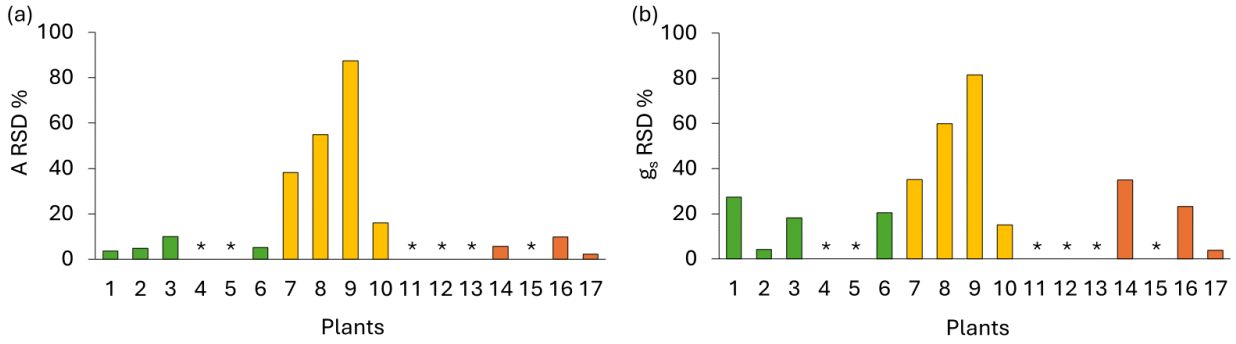

Figure 6. Relative standard deviation (RSD, %) of baseline gas exchange measurements for individual plants (n = 17) across initial, pre-chamber, pre-fumigation PPS measurements. (a) Net CO_2 assimilation (A); (b) stomatal conductance (g_s). Each bar represents variability across baseline measurements for a single plant. Asterisks indicate missing day one values due to scheduling constraints.

Relative percent change for each plant's raw A (µmol m^{-2} s^{-1}) and g_s (mol m^{-2} s^{-1}) from its post- control and fumigation exposure values;

$$Percent\ Relative\ Change_{plant} = \left(\frac{Post - Fumigation_{plant} - Post - Control_{plant}}{Post - Control_{plant}}\right) \times 100\%$$

Figure 7 highlights high variability between A (Figure 7a) and g_s (Figure 7b). Positive values indicate post-fumigation measurement was higher relative to post-control. Plant 3 shows this positive value for A at 15% and plants 3, 5, 13, 15, and 17 for stomatal conductance at 37%, 64%, 18%, 3%, and 3% respectively.

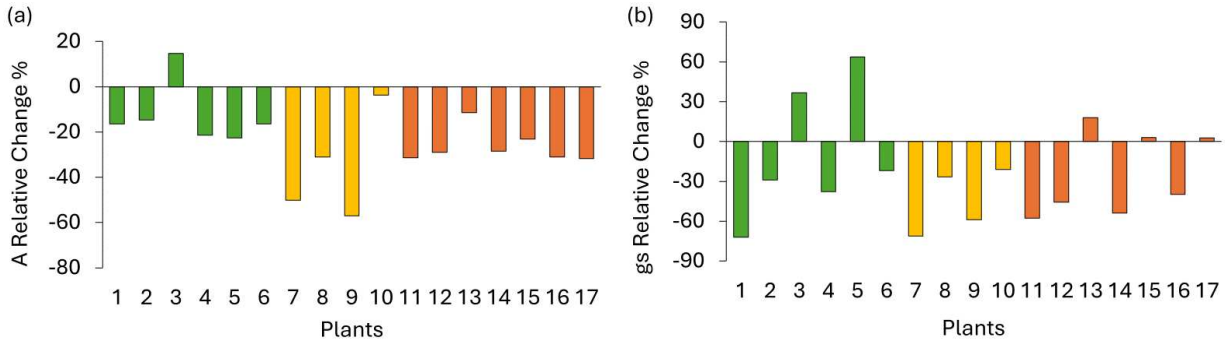

Figure 7. Relative percent change in gas exchange following smoke exposure for individual plants (n = 17), calculated relative to the post-control response. (a) net CO_2 assimilation (A); (b) stomatal conductance (g_s). Each bar represents the percent change (%) for a single plant.

3.1 Leaf-level photosynthetic responses to $PM_{2.5}$ exposure

Changes in ΔA decreased across all smoke treatments (Figure 3a). The control chamber exhibited an average change of -1.0 ±1.2 µmol m^{-2} s^{-1}. In comparison, the low-, medium-, and high-smoke treatments showed larger decreases of -2.6±1.9, -2.5±1.9, and -3.0±1.4 µmol m^{-2} s^{-1}, representing decreases approximately 160%, 150%, and 200% greater than the control response, respectively. The magnitude of response was smaller for Δg_s (Figure 3b); control measurements averaged -0.008±0.033 mol m^{-2} s^{-1}, while the low-, medium-, and high-smoke treatments showed

changes of -0.014±0.032, -0.016±0.010, and -0.014±0.025 mol m^{-2} s^{-1}, representing decreases approximately 75%, 100%, and 75% greater than the control response, respectively.

The magnitude and consistency of these responses align closely with previous studies documenting rapid smoke-induced inhibition of photosynthesis across diverse plant functional types. Gilbert and Ripley[25] reported sharp declines in both A and g_s in *Chrysanthemoides monilifera* following just one minute of smoke exposure, with reductions of up to 66% in A and 80% in g_s within three hours. Similarly, Calder et al.[26] observed greater than 50% reductions in photosynthetic capacity across five of six pine species examined after brief smoke exposures, accompanied by significant decreases in g_s within 30 minutes. Although the exposure durations and species differ, the consistency of reduced gas exchange across studies shows that smoke acts as a potent and rapid stressor to leaf-level physiological function.

3.2 Net smoke effects on leaf gas exchange

The isolated effects of smoke exposure, expressed as net smoke effect, are shown in Figure 5. For A (Figure 5a), mean responses were -0.5±1.6, -1.6±1.9, and -2.1±1.8 μmol m^{-2} s^{-1} for the low-, medium-, and high-smoke treatments respectively. For g_s (Figure 5b), mean responses were -0.03 ±0.09, -0.02 ±0.02, and -0.00 ±0.05 mol m^{-2} s^{-1} for the same treatments.

Across all plants, most responses were negative. For A, 14 of the 17 plants (~82%) showed negative net smoke effects, indicating that most individuals experienced additional suppression under smoke exposure relative to the g_s. The largest suppression of A was observed in one individual plant (−5.5 μmol m^{-2} s^{-1}), while the smallest response was -0.1 μmol m^{-2} s^{-1}. For g_s, responses were less consistent than those observed for A. Thirteen of the 17 plants (~76%) showed negative net smoke effects, indicating that many individuals experienced some reduction in g_s under smoke exposure relative to the chamber control. The largest suppression of g_s was observed

in one individual plant (-0.09 mol m^{-2} s^{-1}), while the smallest response was -0.006 mol m^{-2} s^{-1} (Figure 5b).

A gradual increase in the magnitude of A suppression was observed across smoke treatments (Figure 5a), with mean effects becoming progressively more negative from low to medium to high smoke, despite large error bars. In contrast, g_s showed no consistent concentration-dependent pattern: most plants exhibited small, variable, and non-significant changes, and treatment means had large standard deviations as well. g_s had no statistically significant differences among treatments were detected.

3.3 Relative percent change in gas exchange

Mean relative percent change in A decreased across the smoke treatments and not consistent with increasing $PM_{2.5}$ concentrations. Control plants showed an average change of -12.2 ± 13.9%, while the low-, medium-, and high-smoke treatments showed mean decreases of -21.0 ± 9.7%, -36.4 ± 18.4%, and -29.7 ± 11.6%, respectively (Figure 4a). Mean relative percent changes for g_s were -0.1 ± 43.3% for the control, -9.3 ± 35.8% for low-smoke, -35.8 ± 17.2% for the mid-smoke, and -13.0 ± 31.1% for the high-smoke treatment (Figure 4b). Smoke treatment significantly affected the relative percent change in A ($F_{3,30} = 5.17$, $p = 0.005$) (Figure 4a). Bonferroni post hoc comparisons showed that the medium- and high-smoke treatments differed significantly from the control treatment ($t = 3.26$ and $t = 2.92$, respectively; $P < 0.05$). The low-smoke treatment did not differ significantly from the control, and differences among the smoke treatments themselves were not statistically significant ($t = 1.38$, 1.78, 1.18, and 0.80 for control vs low, low vs medium, low vs high, and medium vs high respectively). Relative percent change in g_s did not differ significantly among treatments ($F_{3,30} = 1.12$, $p = 0.36$). Similarly, analyses of averaged ΔA ($p = 0.14$) and averaged Δg_s ($p = 0.72$) showed no significant differences among smoke treatments.

4. Discussion

4.1 Smoke exposure suppresses CO_2 assimilation.

Smoke exposure reduced leaf-level net CO_2 assimilation relative to chamber control conditions across several analytical metrics. The clearest treatment effect was observed for relative percent change in assimilation, where medium and high smoke treatments were significantly more negative than the control (Figure 4a). Reductions in assimilation occurred even though stomatal conductance did not differ significantly among treatments. Variation among individual plants was evident in the initial gas exchange measurements. For example, Plant 3 had the highest starting assimilation rate ($A = 17.35$ μmol m^{-2} s^{-1}) with a stomatal conductance of ($g_s = 0.11$ mol m^{-2} s^{-1}), whereas Plant 12 had a lower initial assimilation rate ($A = 10.31$ μmol m^{-2} s^{-1}) but the highest stomatal conductance of ($g_s = 0.15$ mol m^{-2} s^{-1}).

Previous smoke exposure studies frequently report concurrent declines in both assimilation and stomatal conductance. For example, Gilbert and Ripley[25], Calder et al.[26], and Riches et al.[27] all observed decreases in both gas-exchange parameters during smoke exposure. However, these studies differed from the present experiment in species, exposure duration, smoke composition, and environmental conditions, all of which may influence plant physiological responses. The divergence between net CO_2 assimilation and stomatal conductance in this study suggests that wildfire smoke may influence photosynthesis through mechanisms that are not solely controlled by stomatal regulation.

4.2 Potential mechanisms to photosynthetic suppression.

Several mechanisms may explain the reductions in assimilation observed during smoke exposure. Corn's C_4 anatomy creates a CO_2-concentrating system that shifts the primary limits on photosynthesis away from stomatal supply and toward the biochemical steps occurring inside the leaf. CO_2 is first fixed in the mesophyll and then delivered at elevated concentration to Rubisco in

the bundle sheath, allowing the leaf to maintain a low internal/atmosphere CO_2 concentration ratio while still supplying Rubisco with abundant substrate. Under typical ambient conditions, C_4 photosynthesis is generally constrained by Rubisco activity rather than by CO_2 diffusion through stomata. Because the internal CO_2 gradient is steep, stomatal conductance can remain relatively low without restricting carbon assimilation, meaning that CO_2 uptake in corn is not usually limited by stomatal behavior and the plant achieves high water-use efficiency while maintaining robust photosynthetic rates.[48]

4.2.1 Stomatal signaling pathways.

Stomatal conductance did not show a consistent treatment response in this study (Figures 3–5), indicating that stomatal signaling alone cannot explain the observed reductions in net CO_2 assimilation. Smoke contains reactive gases and VOCs that activate plant stress-response pathways, including abscisic acid (ABA), a regulator of stomatal closure that can suppress CO_2 uptake via stomatal and non-stomatal mechanisms.[49] Plant water status likely contributed to g_s variability: soil moisture was not monitored and plants were watered once daily. Individual plants may have experienced intermittent water stress that alters photosynthetic behavior at the start of this study.[50] Corn photosynthetic processes typically declines by 5-10% due to soil moisture at 75% field capacity and by more than 50% at 50% field capacity.[51] Corn's C_4 physiology normally buffers assimilation against moderate stomatal limitation, but the findings of Kebede et al.[51] study shows that when stomatal conductance decreases severely under water stress, even a C_4 leaf cannot maintain high assimilation.

Previous studies report smoke-driven impairments of photosynthesis via internal limitations: Gilbert and Ripley[19] found reduced carboxylation efficiency and RuBP regeneration, Calder et al.[20] attributed declines in photosynthetic capacity to combined stomatal and internal

effects, Gaastra[52] showed that mesophyll conductance can constrain CO_2 delivery to the chloroplast even when stomatal conductance is unchanged, and Jajoo et al.[53] observed pollutant-associated compounds that directly impair PSII and electron transport. In our chamber exposures, reduced CO_2 uptake was consistent with predominantly non-stomatal (biochemical or mesophyll diffusion) limitations rather than stomatal closure. The sections that follow evaluate two primary non-stomatal pathways, VOC-driven biochemical and diffusion constraints, and $PM_{2.5}$-driven internal and chemical effects, to interpret the observed decoupling of net CO_2 assimilation and stomatal conductance.

4.2.2 Non-stomatal limitations associated with VOC exposure.

VOC exposure provides a plausible non-stomatal mechanism for the observed suppression of photosynthesis, operating through both internal diffusion constraints and biochemical impairment. Smoke generated from ponderosa pine needles contains a complex mixture of oxygenated organics, phenolics, aromatic acids, and semi-volatile compounds that dynamically partition between gas and particle phases.[54,55] These species can enter the intercellular airspace and aqueous leaf environment without requiring changes in stomatal aperture, consistent with the weak and non-significant responses in g_s observed in Figures 3b and 5b.

Within the leaf, these compounds can limit photosynthesis by reducing mesophyll conductance (g_m) and biochemical processes. Mesophyll conductance governs CO_2 diffusion from the intercellular airspace to the chloroplast, and reductions in g_m can substantially lower chloroplast CO_2 concentration even when stomatal conductance remains constant.[56] Reactive organics in the intercellular airspace may disrupt diffusion pathways or interact with aqueous mediators of CO_2 transport, effectively reducing CO_2 delivery to the sites of fixation. Simultaneously, reactive oxygen species generated from these compounds can inhibit Calvin cycle

enzymes and damage Rubisco and associated proteins, directly reducing the biochemical capacity for carbon fixation.[57–60]

In addition to these effects, polycyclic aromatic hydrocarbons (PAHs), which are abundant in biomass smoke, can directly impair photochemical processes. PAHs are known to partition into thylakoid membranes, disrupting photosystem II, electron transport, and overall chloroplast structure.[53,61] These membrane-level disruptions further constrain carbon assimilation independent of stomatal regulation.

4.2.3 Non-stomatal limitations associated with $PM_{2.5}$ exposure.

$PM_{2.5}$ exposure provides a complementary non-stomatal pathway for photosynthetic suppression through physical entry into the leaf, internal deposition, and sustained chemical interactions within leaf tissues. Fine particles can access internal spaces via stomata; Chen et al.[32] demonstrated $PM_{2.5}$ penetration into stomatal regions to depths of ~5–14 μm, allowing particles and associated compounds to reach substomatal cavities and near-mesophyll environments. This pathway enables internal exposure without requiring changes in stomatal aperture, consistent with the weak g_s responses observed in Figures 3b and 5b.

Once deposited, the chemical composition of $PM_{2.5}$ governs its impact. Biomass-derived particles contain inorganic ions (e.g., sulfate, nitrate, ammonium) and a mixture of organic compounds, including semi-volatile species and PAHs.[18,44,62] These components can dissolve or react within aqueous leaf phases.[61] Increasing $PM_{2.5}$ concentrations also elevate particle loading on leaf surfaces and within stomatal regions,[18,63] creating a concentration-dependent increase in internal exposure. The progressive decline in assimilation across treatments, despite minimal changes in g_s, is consistent with increasing particulate load driving internal, rather than stomatal, limitation. Particles retained within stomatal cavities and substomatal spaces can also function as

localized chemical reservoirs. Semi-volatile and low-volatility compounds partition dynamically between particle and gas phases and exchange with the surrounding microenvironment.[54,55] This sustained exposure can prolong interactions with mesophyll tissues even after external concentrations decrease.

Together, these mechanisms highlight the decoupling observed in this study, A declined substantially while g_s showed little to no change. This pattern indicates that internal limitations, particularly reduced mesophyll conductance and biochemical impairment, dominate over stomatal control under these exposure conditions. In maize, a C_4 species that typically sustains high assimilation at lower stomatal conductance, disruption of mesophyll biochemical capacity or thylakoid function weakens the CO_2-concentrating mechanism itself.[48] When this internal machinery is compromised, A declines disproportionately relative to g_s. The magnitude and progression of assimilation suppression across $PM_{2.5}$ treatments align with this framework, supporting a primarily non-stomatal origin for the observed declines.

4.3 Experimental limitations

Several experimental factors contributed to variability in physiological responses. Transfer into the control chamber produced a measurable chamber effect: most plants (14 of 17) showed declines in assimilation after control exposure (0.2–6.6 μmol m^{-2} s^{-1}), and 10 of 17 showed declines in stomatal conductance (0.002–0.056 mol m^{-2} s^{-1}). Chamber-induced changes in gas exchange are well documented and can arise from altered airflow, light quality or intensity, and enclosure stress.[8,64] These effects introduce baseline shifts in both net CO_2 assimilation and stomatal conductance, increasing variability and reducing sensitivity to treatment-specific responses.

Plant water status was not fully uniform across experimental days. Although plants were watered regularly, variation in watering timing and occasional missed waterings likely altered leaf

water potential among individuals. Because stomatal conductance is highly sensitive to water status,[51] this variability would increase values in g_s and obscure any consistent stomatal response to smoke exposure, contributing to the weak and non-significant stomatal trends observed in this study.

Baseline physiological condition also appeared lower than that of well-watered corn. Kebede et al.[51] reported net CO_2 assimilation rates near 25 µmol m^{-2} s^{-1} at full soil moisture, with declines of ~7% at 75% field capacity and ~55% at 50% field capacity. Net CO_2 assimilation in the present study was generally below ~25 µmol m^{-2} s^{-1}, consistent with moderate pre-existing stress. Reduced baseline capacity may both lower absolute photosynthetic rates and decrease sensitivity to additional stressors such as smoke exposure. These experimental limitations introduce variability in physiological measurements and should be considered when interpreting the magnitude and variability of the observed responses. However, the consistent reduction in assimilation across smoke treatments remains a robust outcome of this study.

4.4 Ecological and agricultural implications

The consistent reduction in assimilation observed in this study suggests that wildfire smoke exposure may directly reduce carbon uptake in agricultural corn systems. Short-term decreases in leaf-level CO_2 assimilation can reduce cumulative carbon gain if exposure is repeated or occurs during critical developmental stages. Thompson et al.[65] demonstrated that ambient photochemical pollutants, including ozone, reduced plant growth, biomass, and ear development in sweet corn, with substantial declines in kernel set and marketable yield. These effects were associated with impaired leaf function and premature senescence, the degradation of the photosynthesis apparatus for relocation of nutrients to the grain,[66] indicating that reductions in photosynthetic capacity can directly translate into reduced agricultural productivity. At larger scales, similar relationships have

been observed between air pollution and crop yield. Zhou et al.[17] reported significant negative relationships between $PM_{2.5}$ concentrations and crop yields across multiple regions in China for wheat and corn, while Dillis et al.[67] estimated that wildfire smoke exposure caused crop losses exceeding $1 billion in California's cannabis industry during severe wildfire seasons.

4.5 Future work

Future studies should aim to more clearly separate stomatal and non-stomatal controls on photosynthetic suppression during smoke exposure. While gas-exchange measurements alone cannot fully distinguish between mesophyll and biochemical limitations, the observed pattern strongly supports a non-stomatal pathway. Future measurements, including CO_2 response curve (A/C_i) with mesophyll CO_2 conductance (g_m) estimation, chlorophyll fluorescence, and chemical analysis of smoke source's particulate matter and gases, would further resolve the relative contributions of these mechanisms. The LI-COR 6800 PPS can measure a CO_2 response curve with mesophyll CO_2 conductance (g_m), and chlorophyll fluorescence parameters: F_v/F_m for maximum quantum efficiency of PSII and $\Delta F/F_m$ for PSII efficiency.

Improved experimental control may also reduce variability in stomatal responses. Growing corn from seeds specifically for chamber experiments would ensure more uniform developmental stages and physiological conditions at the time of exposure. Maintaining one plant per pot and implementing an automated watering system would help standardize plant water status prior to fumigation. Increasing the plant number per concentration group would help with plant variability when averaging plant values with having a set of plants that aren't exposed to fumigation. Finally, microscopy of exposed leaf surfaces could determine whether $PM_{2.5}$ accumulates within stomatal pores during smoke exposure.

5. Conclusion

Across all treatments, smoke reduced net CO_2 assimilation, with the strongest and most statistically significant declines observed in the medium and high $PM_{2.5}$ conditions by relative percent change. Control plants showed an average A change of -12.2 ± 13.9%, while the low-, medium-, and high-smoke treatments showed mean decreases of -21.0 ± 9.7%, -36.4 ± 18.4%, and -29.7 ± 11.6%, respectively. g_s relative percent changes were -0.1 ± 43.3% for the control, -9.3 ± 35.8% for the low-smoke treatment, -35.8 ± 17.2% for the mid-smoke treatment, and -13.0 ± 31.1% for the high-smoke treatment. The net smoke effect for A mean responses were -0.5±1.6, -1.6±1.9, and -2.1±1.8 μmol m^{-2} s^{-1} for the low-, medium-, and high-smoke treatments respectively. For g_s, mean responses were -0.03 ±0.09, -0.02 ±0.02, and -0.00 ±0.05 mol m^{-2} s^{-1} for the same treatments. A suppression was observed across smoke treatments with net smoke effect values becoming progressively more negative from low to medium to high smoke. In contrast, g_s showed no consistent concentration-dependent pattern.

The results indicate that reductions in photosynthesis were not driven primarily by stomatal closure. We believe the observed patterns support a predominantly non-stomatal mechanism, where disruption in internal processes lead to the decline in net CO_2 assimilation. Integrating these findings with the proposed mechanisms, we hypothesize that both VOCs and $PM_{2.5}$ contribute to internal limitations by reducing mesophyll conductance and impairing biochemical function. Reactive organic compounds and particle-associated species likely disrupt CO_2 diffusion within the leaf and interfere with key photosynthetic processes, including Calvin cycle activity and electron transport. In corn, a C_4 species that typically maintains high assimilation even at relatively low stomatal conductance, these internal disruptions weaken the CO_2-concentrating mechanism itself, leading to disproportionate declines in assimilation.

Therefore, we believe wildfire smoke suppresses photosynthesis in maize primarily through non-stomatal mechanisms, specifically internal diffusion constraints and biochemical impairment, rather than through stomatal closure. This finding refines our understanding of plant responses to atmospheric pollution and highlights the importance of considering internal physiological processes when evaluating the impacts of wildfire smoke on agricultural productivity.

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