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Nitrogen allocation in $PM_{2.5}$ smoke-exposed plants: implications for ecosystem nitrogen cycling and stress response

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Abstract

Background With the increase in forest fire emissions, an increasing amount of nitrogen is released from combustibles and taken up by plant leaves in the form of $PM_{2.5}$ smoke deposition. Concurrently, the stress from $PM_{2.5}$ also disrupts the physiological processes of plants. This study aims to reveal the migration paths of N in combustibles in smoke and plants during forest fires and the stress response of plant leaves to smoke particle deposition. This study conducted a simulated smoke deposition treatment on *Schima superba* and *Cunninghamia lanceolata*, analyzing the changes in plant ^{15}N content and stress-related products.

Results The main findings include the following: (1) Nitrogen in combustibles can be transported to plant leaves via $PM_{2.5}$ smoke during combustion and can be allocated and assimilated in various parts of the plant after being absorbed by the leaves. (2) The stress response of *Schima superba* to $PM_{2.5}$ is less pronounced than that of *Cunninghamia lanceolata*. (3) Under $PM_{2.5}$ stress, the correlation between nitrogen accumulation in the leaves of *Schima superba* and *Cunninghamia lanceolata* and their respective stress responses differs.

Conclusions In forest fires involving different tree species, there are variations in the migration pathways of nitrogen and the stress effects of $PM_{2.5}$ on leaves, with a significant correlation observed between leaf nitrogen accumulation and stress response.

Keywords Forest fire, Smoke, Nitrogen, Malondialdehyde, Zeatin, Abscisic acid

Resumen

Antecedentes Con el incremento de las emisiones generadas por los incendios forestales, una cantidad incremental de nitrógeno es liberado por los combustibles vegetales y tomado por las hojas de las plantas en la forma de deposiciones de humo $PM_{2.5}$ (materia particulada). Concurrentemente, el estrés de $PM_{2.5}$ disrumpe también los procesos fisiológicos de las plantas. Este estudio se enfoca en revelar los patrones de migración del N de combustibles vegetales a humo y plantas durante incendios forestales y el estrés de respuesta de las hojas a la deposición de partículas de humo. En este estudio se condujo un tratamiento de deposición simulada en Schima superba y Cunninghamia lanceolata, analizando los cambios en el contenido de N^{15} y los productos relacionados al estrés producido por esa deposición.

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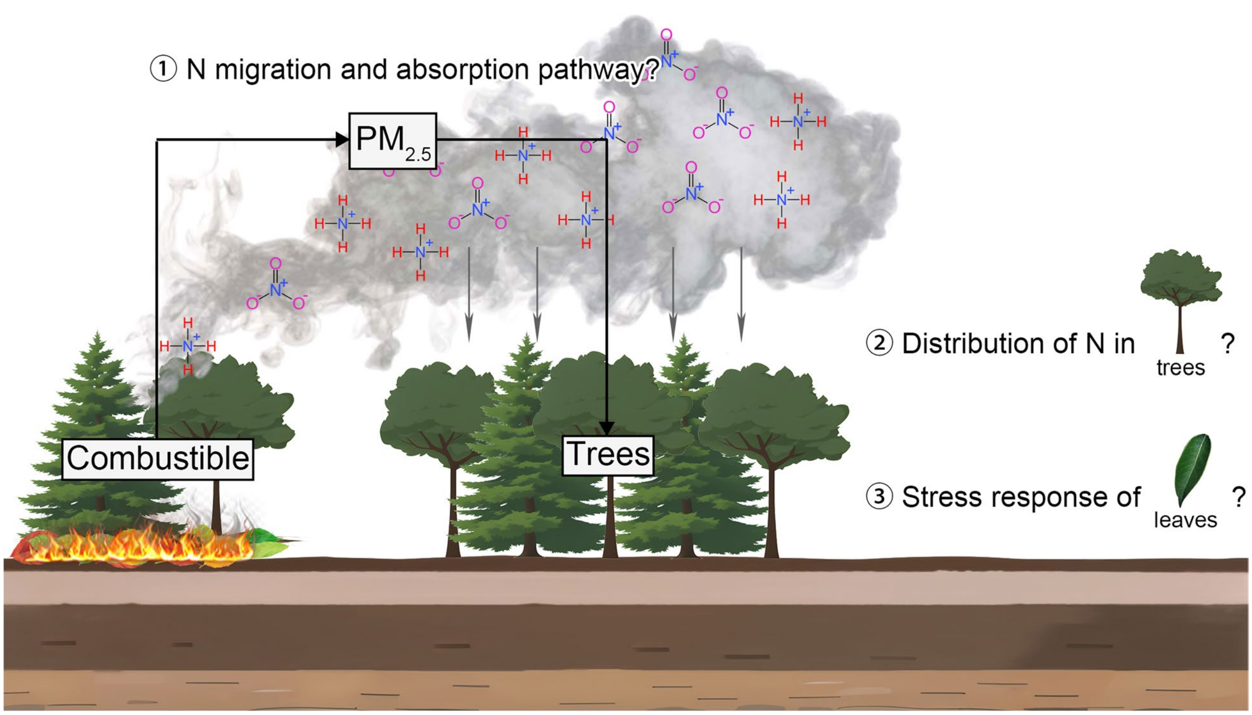
Resultados Los principales resultados incluyen: (1) el nitrógeno de los combustibles puede ser transportado a las hojas de las plantas vía partículas de humo $PM_{2.5}$ durante la combustión, y puede localizarse y ser asimilado en varias partes de las plantas luego de ser absorbido por las hojas. (2) El estrés como respuesta al $PM_{2.5}$ fue menos pronunciado en Schima superba que en aquella ocurrida en Cunninghamia lanceolata. (3) Bajo el estrés producido por $PM_{2.5}$, la correlación entre la acumulación de N en las hojas de Schina superba y Cunninghamia lanceolata difiere en la respuesta al estrés producido entre ambas especies.

Conclusiones En incendios forestales que incluyen diferentes especies, hay variaciones en el patrón de migración del nitrpogeno y los efectos del estrés en las hojas, con una correlación significative entre la acumulación de nitrógeno en las hojas y el nivel de respuesta al estrés.

Graphical Abstract



Background

As global climate change and human activities intensify, forest fires are becoming increasingly frequent worldwide, exacerbating the release of smoke pollutants, including substantial nitrogen (N) emissions into the atmosphere (Andreae 2019). N emissions, primarily in the form of gases such as NO and NO_2 (Jaiswal et al. 2022), have a total emission factor of up to 3 g/kg in forest fires (Andreae 2019). Globally, NO_2-N emissions from biomass burning amount to 0.7 Tg per year, equivalent to N emissions from industrial and fossil fuel combustion (Davidson et Davidson and Kanter 2014). The emission of NO_x and its derivatives can promote the depletion of the ozone layer and cause acid rain, while also causing serious harm to the human respiratory system (Boningari and Smirniotis 2016). With increasing research on forest fire emissions, related research on N emissions in smoke particles has gradually received attention. Smoke particles, primarily $PM_{2.5}$, are a significant component of atmospheric deposition (Jaffe et al. 2020), with emissions in most parts of the world exceeding those caused by human activities (Knorr et al. 2017). Each year, forest fires alone cause 44 million people to be exposed to $PM_{2.5}$ polluted areas ($PM_{2.5} > 55$ μg/m^3), with 4 million considered to be at high health risk ($PM_{2.5} > 250$ μg/m^3) (Roberts and Wooster 2021). N in smoke particles mainly exists in the form of NO_2^-, NO_3^-, and NH_4^+ (Adam et al. 2021), which can account for 84% of the total N mass in particles (Dong et al. 2021). In the actual process of forest fires, smoke particles carrying N can migrate and settle in other areas with atmospheric movement (Hung et al. 2020). According to statistics, forest fire smoke causes an average annual atmospheric N deposition of 0.2 kg/ha in the USA alone (Koplitz et al. 2021), with N deposition in some areas even reaching 16.9 kg/ha per year (Campbell et al. 2022). N deposited on the forest floor with particles interferes with soil microbial activity and nutrient cycling processes dominated by microbes (He et al. 2021), affecting plant growth and development. Appropriate N input can alleviate nutrient limitations in ecosystems, but excessive N deposition will cause negative impacts such as soil pollution and eutrophication of water bodies (Schmitz et al. 2019). Therefore, exploring the emission of N in forest fire smoke particles is of great significance for revealing the N input of forest ecosystems by forest fires.

N is one of the most crucial elements in the global biogeochemical cycle (Schmitz et al. 2019) and is a significant limiting factor for primary productivity and vegetation growth in forest ecosystems (Fan and Yang 2003). As global N emissions and deposition increase, atmospheric deposition has gradually become one of the main input pathways for N in forest ecosystems (Da Ros et al. 2023). Currently, in addition to being absorbed by roots through deposition on the ground, the importance of leaf absorption under atmospheric deposition is gradually being recognized (Guerrieri et al. 2021). Compared with roots, N absorbed by leaves can also have a significant impact on plant growth and development (Moreira et al. 2017), but excessive accumulation of particles on the leaf surface will also cause mechanical damage to the leaves and stomatal blockage (Song et al. 2015). At present, research on the N cycle mainly focuses on specific processes such as N emissions, atmospheric N diffusion and deposition, and plant root absorption of N (Jaffe et al. 2020; Rennenberg and Dannenmann 2015), while there have been many reports on the impact of N on plant physiological processes (Chen et al. 2021; Sun et al. 2020). However, there are few reports on the complete cycle of "emission-deposition-plant absorption" of N and the impact of particle stress on leaf N absorption and stress response.

In the field of atmospheric research, scholars worldwide have been utilizing N 15 isotope (^{15}N) technology to trace the sources of atmospheric N and its distribution process (Saud et al. 2022). During a forest fire, N in combustibles can enter plants with smoke particles. N isotope analysis technology can be used to explore the migration paths of N during forest fires, leaf absorption of N, and allocation of N in plants based on changes in ^{15}N content in combustibles, smoke particles, and plants. *Cunninghamia lanceolata (Lamb.) Hook.* is the main artificial forest tree species in southern China (Farooq et al. 2019), while *Schima superba Gardn. et Champ.* has good fire resistance and is a major tree species for constructing biological fire prevention belts around artificial forests (Cui et al. 2019). In view of this, this study selected *Schima superba* and *Cunninghamia lanceolata*; used smoke simulation deposition experiments to determine the migration rate of ^{15}N during smoke release, deposition, and leaf absorption and the allocation rate of ^{15}N in plants; and analyzed the impact of particle stress on leaf absorption and intraplant migration of N and the release of stress response products. This study aims to reveal the migration paths of N in combustibles in smoke and plants during forest fires and the stress response of plant leaves to smoke particle deposition. It provides a scientific basis for studying the impact of smoke deposition on the N cycle of ecosystems.

The scientific hypotheses proposed in this article are as follows: (1) During forest fires, N has a migration and absorption process of "combustibles-smoke-leaves-roots." (2) N absorbed through the leaves is first transported to growth-critical parts, such as leaves or stems. (3) Under smoke stress, the plant's stress response promotes the accumulation of N in the leaves, enhancing its resistance.

Methods

Test material

The 3-year-old *Schima superba* and *Cunninghamia lanceolata* seedlings used in the experiment were sourced from the Youxi County State-owned forest farm. The seedlings were healthy, with no signs of damage or pest infestation. After removing the seedling matrix bag, the roots were rinsed with pure water and planted in polyethylene plastic flower pots filled with washed river sand. The seedlings were acclimated for half a month. Each seedling was regularly and quantitatively treated with Hoagland nutrient solution and watered with pure water.

Test procedure

Isotopic labeling of combustibles

Selected *Schima superba* and *Cunninghamia lanceolata* seedlings were used for isotope labeling. The labeled N was $^{15}NH_4^+$ with isotopes, with a labeling amount of 30 mg ^{15}N per plant. The labeled N was made into a solution and evenly injected into the soil using a syringe. The micro-injection method was used for fertilization labeling, with four holes in the outer layer, five holes in the middle layer, and one hole in the center, to ensure even distribution of the solution in the soil. All N was labeled in five applications within 5 days. To avoid differences in pollutants released by combustibles with different water contents during combustion, the day after isotope labeling was completed, the labeled seedlings were placed in a 65 °C oven and dried to constant weight.

Smoke simulation deposition

A custom-designed smoke deposition simulation device was utilized to simulate smoke deposition on *Schima superba* and *Cunninghamia lanceolata* seedlings (Fig. 1). The device comprises three parts: a movable combustion chamber, a smoke deposition chamber, and a smoke detection equipment. The movable combustion chamber is a cubic box with a side length of 0.5 m, equipped with a temperature controller that can raise the temperature in the box to 200 ~ 300 °C and keep it constant. The smoke deposition chamber is a closed space covered with polyethylene film. The overall shape is a hexagonal prism with a side length of 1 m and a height of 2.5 m, and it has a pointed top. There are six fans in the room that can evenly distribute the smoke. The smoke detection instrument is connected to the smoke deposition chamber through pipes. It mainly includes an SKC-DPS particle sampler (SKC Inc., USA) and a TSI8533 particle analyzer (TSI Inc., USA), which can collect and analyze the particulate matter in the smoke in the deposition chamber. In addition, the Testo350 smoke analyzer (Testo SE & Co. KGaA, Germany) can also monitor the flue gas through this pipe to verify the combustion state.

Twenty healthy seedlings with similar growth were evenly placed in the deposition chamber, arranged in such a way that their tree crowns covered as much ground as possible without overlapping. In an effort to simulate the smoke emissions produced by actual forest fires, a comprehensive field survey was conducted within the forest. This allowed us to ascertain the quantity of actual combustible materials present within the area encompassed by the smoke deposition chamber. Following a series of preliminary tests for validation, we designated two groups for our study: a control group (CK) which used 0 g of combustibles and a treatment group (T) which used 100 g of combustibles, to simulate smoke deposition. To ensure the complete burning of both *Schima superba* and *Cunninghamia lanceolata* combustibles and a stable flame state, the temperature of the combustion chamber was set to 300 °C. After preheating the combustion chamber, the temperature in the chamber was maintained at 300 °C within 5 min and the combustibles were burned. The released smoke was fully mixed by the fan in the deposition chamber and settled on *Schima superba* and *Cunninghamia lanceolata* seedlings. The CO_2 and CO concentrations in the smoke were measured using a Testo350 smoke analyzer to verify if the combustion efficiency MCE of *Schima superba* and *Cunninghamia lanceolata* combustibles was similar. After 24 h of smoke treatment, the deposition chamber was opened and sampled after the smoke had naturally dissipated. The formula for combustion efficiency MCE is as follows.

$$\mathrm{MCE} = \frac{\Delta \mathrm{CO_2}}{\Delta \mathrm{CO_2} + \Delta \mathrm{CO}}$$

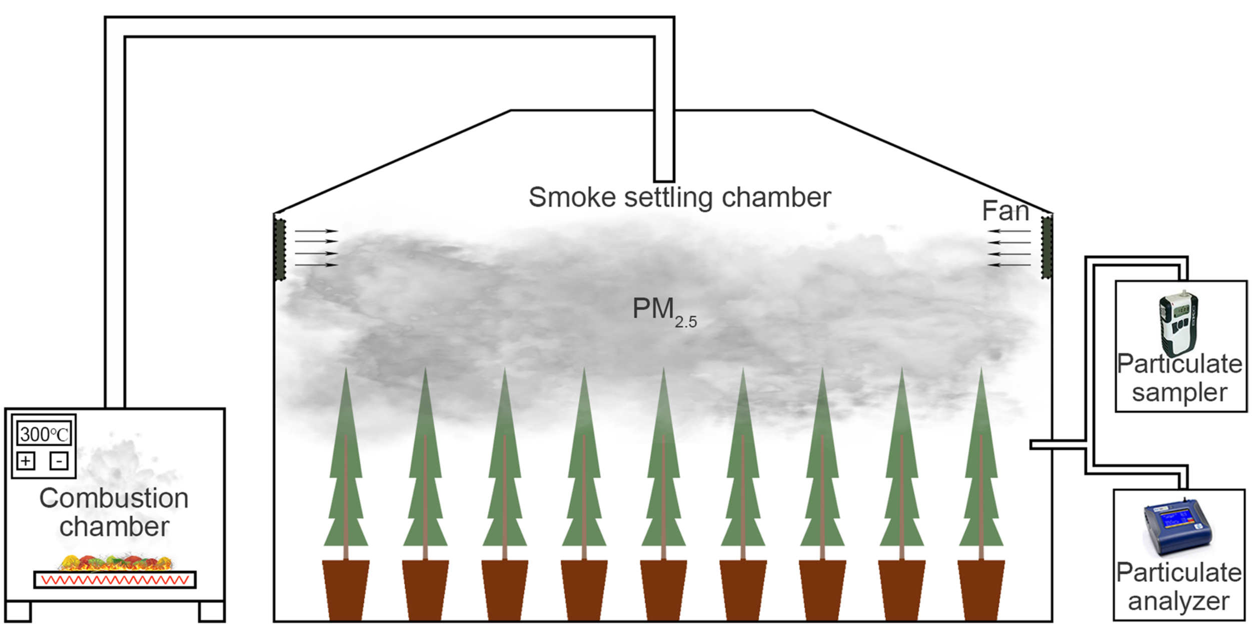


Fig. 1 Schematic diagram of the smoke deposition simulation device

In the formula, ΔCO_2 and ΔCO represent the changes in CO_2 and CO concentrations during combustion, respectively. Generally, a combustion state with an MCE between 0.85 and 0.99 can be considered as flaming combustion.

Determination of N content and ^{15}N abundance

The N content and ^{15}N abundance in combustibles, smoke particles, and seedlings were determined using the Elementar Isoprime vario ISOTOPE cube Elemental Analyzer (Elementar Analysensysteme GmbH, Germany) in conjunction with the Elementar isoprime 100 Stable Isotope Ratio Mass Spectrometer (Elementar Analysensysteme GmbH, Germany) (Ferretti et al. 2017). For combustibles, all samples were dried at 65 °C, thoroughly mixed, and then ground with a grinder. A portion of the dry combustibles was sieved through a 100-mesh sieve for the N content and ^{15}N abundance measurement. Simultaneously, 100 g of dry combustibles were weighed for subsequent combustion. For smoke particles, an SKC-DPS particle sampler was used to collect mixed smoke in the deposition chamber (Ma et al. 2021). The collected samples were then measured for the N content and ^{15}N abundance. In parallel, a TSI8533 particle analyzer was used to measure the $PM_{2.5}$ concentration of the mixed smoke to calculate the total mass of $PM_{2.5}$ (Ma et al. 2022). For seedlings, samples after 1, 7, and 15 days of smoke treatment were divided into aboveground and belowground parts. They were cleaned in a beaker containing 200 ml of ultrapure water using an ultrasonic cleaner and a glass rod. After cleaning, they were dried in a 65 °C oven. Then, the N content and ^{15}N abundance of the seedlings are measured, and their dry weight is also determined.

Determination of malondialdehyde and plant hormone levels

Seedling leaves were collected 1, 7, and 15 days after smoke treatment and preserved in a dry ice cooler for subsequent laboratory analysis. The malondialdehyde (MDA) content in the leaves was determined by the thiobarbituric acid (TBA) method (Morales and Munné-Bosch 2019), while the contents of zeatin (ZA) and abscisic acid (ABA) were determined by high-performance liquid chromatography (HPLC) (Ciha et al. 1977; Zhang et al. 2019).

Statistical analysis

In this study, Excel 2019 was used to organize and analyze the experimental data, including calculating the mean and standard error of the migration rate and allocation rate of ^{15}N, endogenous hormones in plant leaves, etc. SPSS 22 (Cetinkaya and Kulak 2019) was used to perform a one-way analysis of variance (one-way ANOVA) on the experimental data, as well as correlation analysis (Pearson correlation coefficient) based on the accumulation of ^{15}N in leaves and the content of malondialdehyde, the accumulation of ^{15}N in leaves and the content of Zeatin, and the accumulation of ^{15}N in leaves and the content of abscisic acid. OriginPro 2022 was used for graphing.

Results

Pathways of N migration and uptake

The migration rate of ^{15}N varies at different stages of the migration path (Fig. 2). This study found that during the combustion of *Schima superba*, the ^{15}N migration rates in the "litter-$PM_{2.5}$" and "$PM_{2.5}$-plant" processes were 23.19% and 39.23%, respectively. However, during the combustion of *Cunninghamia lanceolata*, the rates were 6.76% and 40.47%, respectively.

N uptake and distribution by plants

The N content of plants is influenced by smoke deposition (Fig. 3). This study discovered that the N content of both *Schima superba* and *Cunninghamia lanceolata* increased after the smoke from combustible materials deposited on their leaves. In comparison with the blank control group (C), the N content of the *Schima superba* smoke treatment group (T) increased by 5.83%, 8.07%, and 11.10% on the 1st, 7th, and 15th days after smoke treatment, respectively. Meanwhile, the increases for *Cunninghamia lanceolata* were 5.43%, 5.23%, and 6.05%, respectively.

The allocation rate of ^{15}N in plants changes over time (Fig. 4). This study discovered that the ^{15}N allocation rates in the aboveground and belowground parts of *Schima superba* ranged between 89.2 ~ 92.4% and 7.6 ~ 10.8%, respectively. In contrast, for *Cunninghamia lanceolata*, the rates ranged between 62.4 ~ 68.2% and 31.8 ~ 37.6%, respectively. From 1 to 15 days post-smoke treatment, the ^{15}N allocation rate in the aboveground parts of both *Schima superba* and *Cunninghamia lanceolata* increased over time, while the rate in the belowground parts decreased.

Stress responses of plants to $PM_{2.5}$ stresses

The MDA content in plant leaves exhibits significant differences under various smoke deposition treatments (Fig. 5). For *Schima superba*, the MDA content slightly increased within the first 1 ~ 7 days compared to the control group but then significantly decreased on the 15th day. In contrast, the MDA content of *Cunninghamia lanceolata* remained relatively stable on the first day but showed a significant increase on the 7th and 15th days, with the increment also demonstrating an upward trend.

The endogenous hormone content in plant leaves exhibits significant differences under various smoke

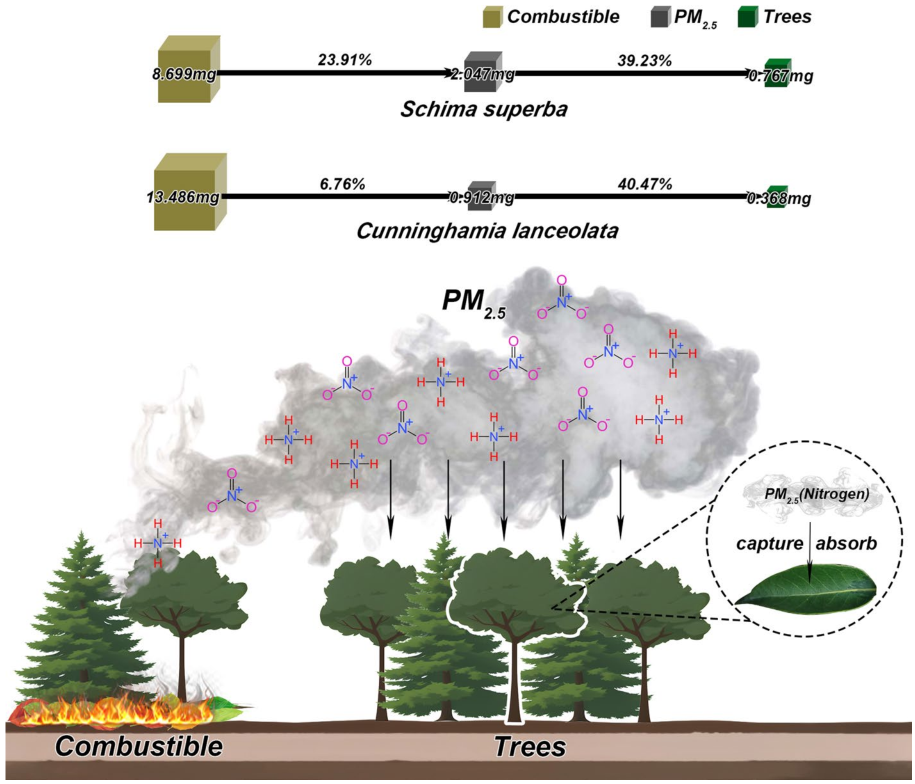


Fig. 2 Comparison of ^{15}N migration rates between *Schima superba* and *Cunninghamia lanceolata*

deposition treatments (Fig. 5). For *Schima superba*, compared to the control group, the ZA content slightly increased on the first day and then returned to normal levels. In contrast, the ZA content of *Cunninghamia lanceolata* significantly decreased on the first day and then significantly increased on the 7th and 15th days. Post-smoke deposition, the ABA content of both tree species significantly increased compared to the control group, but their trends varied. The ABA content of *Schima superba* did not change significantly on the first day, but showed a significant increase on the 7th and 15th days, with a downward trend in its increment. The ABA content of *Schima superba* may return to normal levels. However, the increment of *Cunninghamia lanceolata* ABA content remained at a high level without any recovery trend.

Effects of plant stress on leaf N uptake and accumulation

The correlation between the accumulation of ^{15}N in leaves of different tree species and the content of MDA exhibits varying changes (Fig. 6). For *Schima superba*, there is no significant correlation between the accumulation of ^{15}N in the leaves and the content of MDA ($r = -0.019$). However, for *Cunninghamia lanceolata*, a significant negative correlation exists between the accumulation of ^{15}N and the content of MDA ($r = -0.785^{*}$).

The correlation between the accumulation of ^{15}N in the leaves of different tree species and the content of endogenous hormones exhibits varying changes (Fig. 6). For *Schima superba*, there is a significant positive correlation between the accumulation of ^{15}N and the ZA content ($r = 0.611^{*}$) but no significant correlation with the ABA content ($r = 0.305$). However, for *Cunninghamia lanceolata*, there is no significant correlation between the accumulation of ^{15}N and the ZA content ($r = -0.503$), but a significant negative correlation exists with the ABA content ($r = -0.768^{*}$).

Discussion

Pathways of N migration and uptake

Smoke contains particles of various sizes (PM_{10}, $PM_{2.5}$, $PM_{0.1}$, etc.), among which only $PM_{2.5}$ can be retained in large quantities on plant leaves. According to statistics, the number of $PM_{2.5}$ retained on the leaf surface can account for more than 90% of the total number of particles (Songting et al. 2014; Tomašević et al. 2005), so this study chose to measure the ^{15}N content in $PM_{2.5}$. N in plants is a key component of amino acids and proteins and is also present in large quantities in important

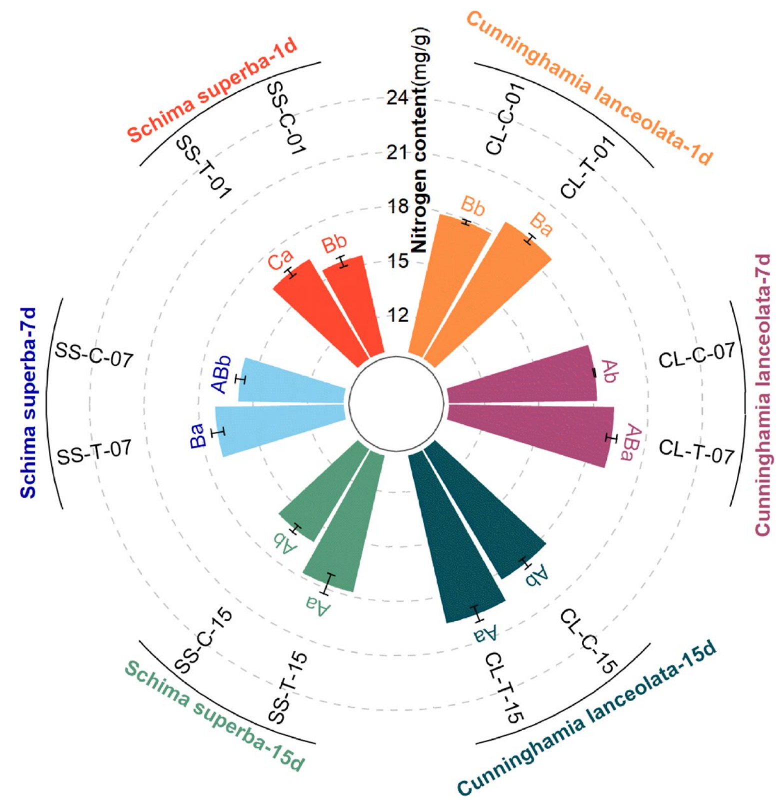


Fig. 3 Changes in N content of *Schima superba* and *Cunninghamia lanceolata* under smoke deposition. The letters "a, b, c, and d" and "A, B, C, and D" represent significant differences between the different smoke treatments and different days, respectively, i.e., $p < 0.05$

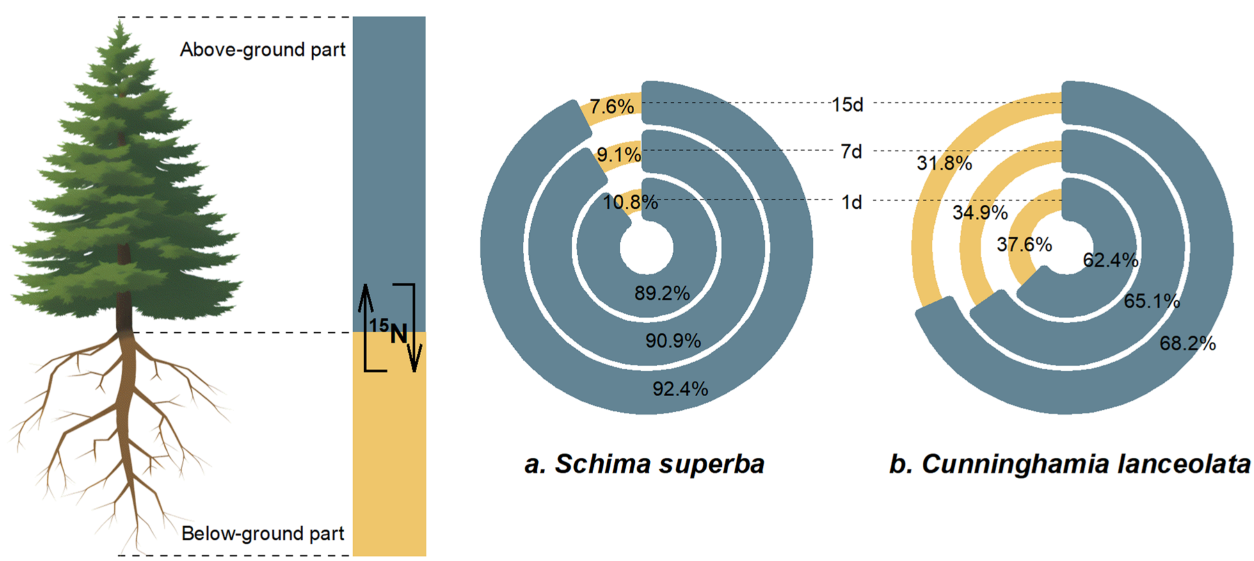


Fig. 4 Changes in ^{15}N distribution rate in *Schima superba* and *Cunninghamia lanceolata* after smoke deposition

biomolecules such as chlorophyll, ATP, and nucleic acids (Fathi 2022). As leaves fall and burn, these N elements undergo complex reactions in the combustion environment and eventually migrate in different forms such as gaseous N, ash residual N, and particulate N (Ozgen et al. 2021; Zhai et al. 2021). Among them, N is

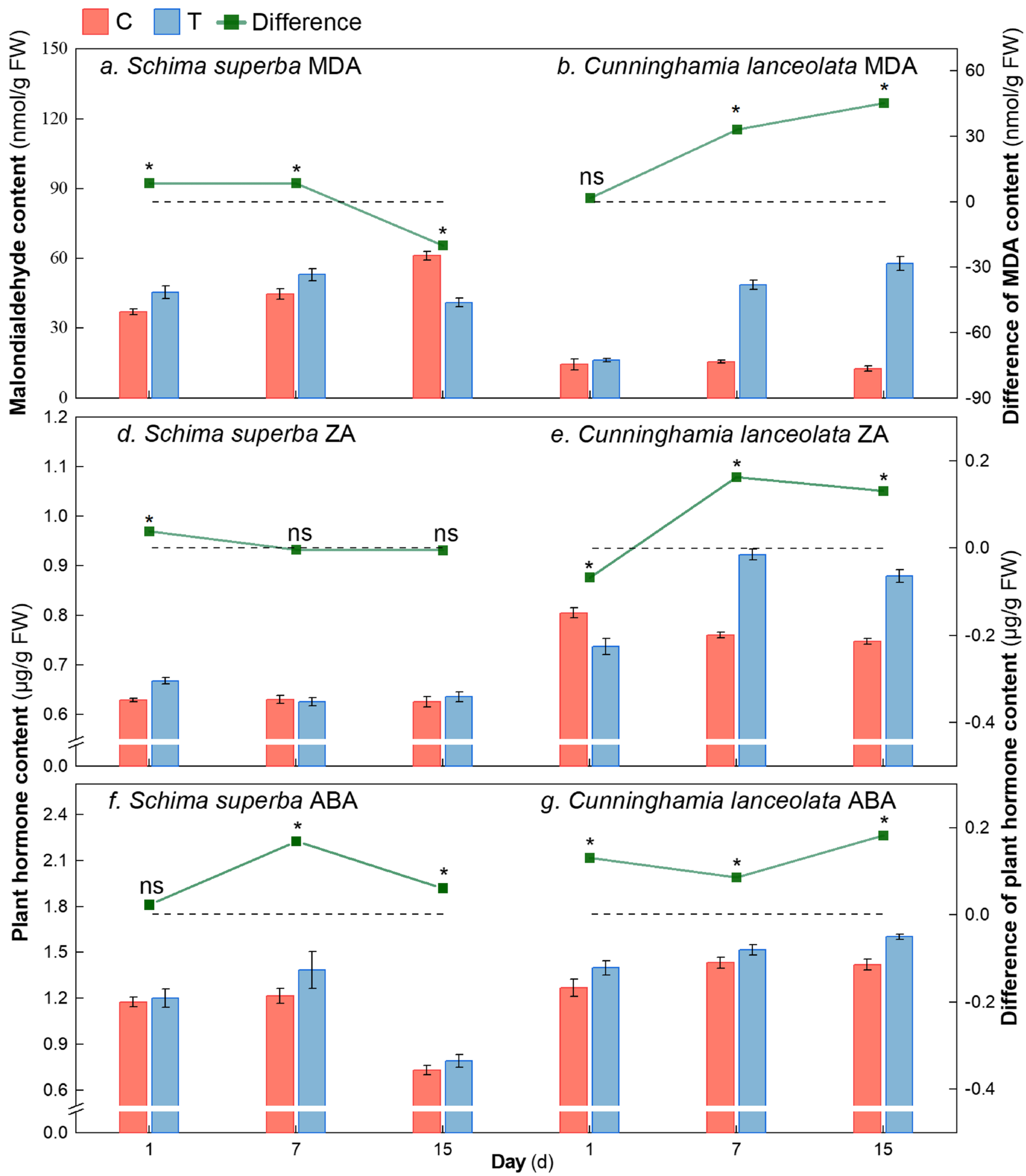


Fig. 5 Changes in malondialdehyde and plant hormone content of *Schima superba* and *Cunninghamia lanceolata* under smoke stress

mostly emitted in the form of gases such as NO_x, and relatively less is emitted with particles such as $PM_{2.5}$ (Ma et al. 2020). Therefore, the results of this study show that the ^{15}N migration rate between litter and $PM_{2.5}$ of both tree species is low (6.76 ~ 23.1%). At the same time, the migration rate between *Schima superba* litter and smoke (23.91%) is significantly higher than that of *Cunninghamia lanceolata* (6.76%), which is caused by the difference in emission characteristics between the two tree species. When the combustion temperature is high, more

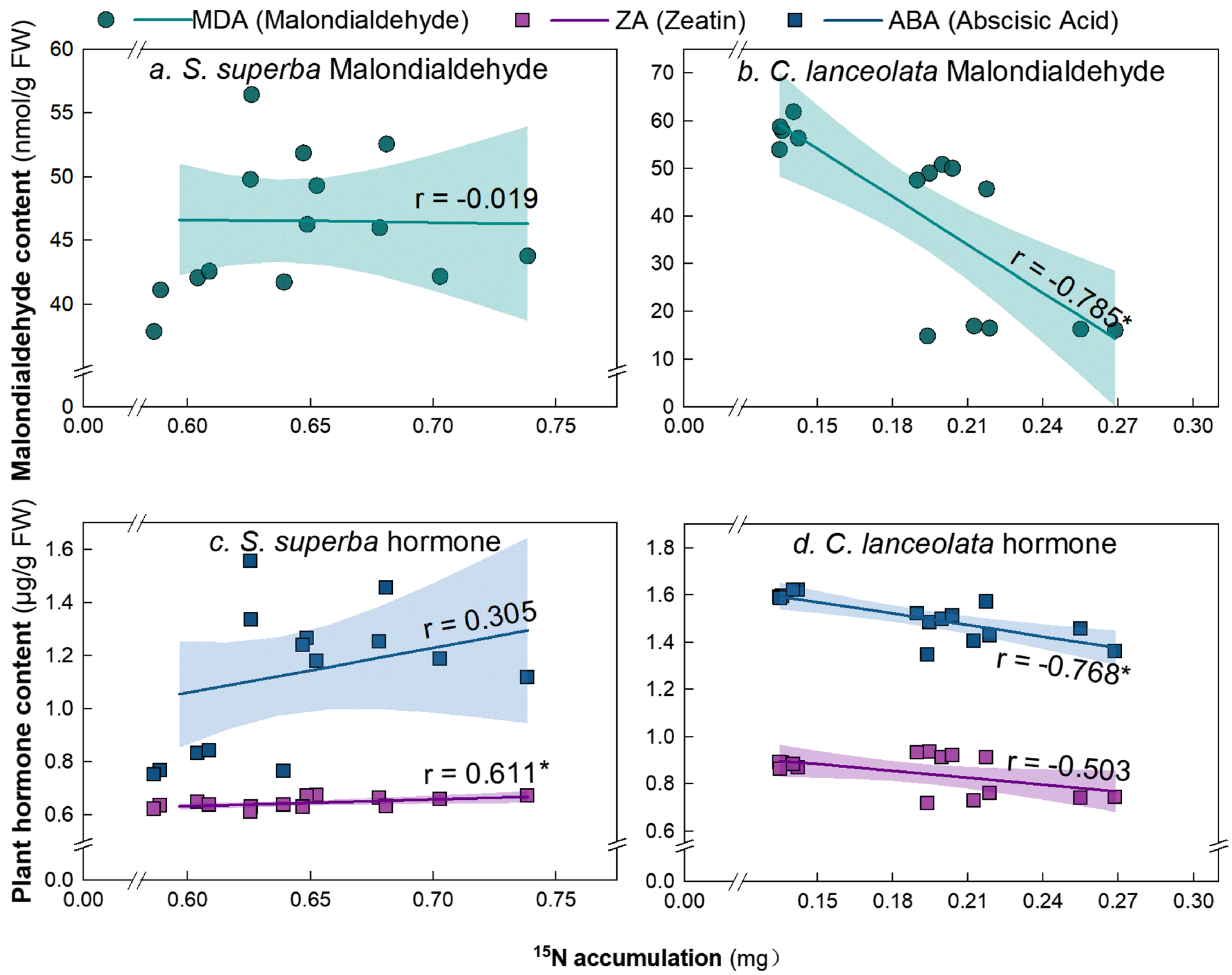


Fig. 6 Correlation between N element accumulation and malondialdehyde and plant hormone content under smoke stress

NO_x is produced by volatilization, pyrolysis, cracking, oxidation, and other processes of combustible N, and the production of liquid and solid particle precursors is inhibited (Demirbas and Arin 2002; Ozgen et al. 2021). Since *Schima superba*, as a fire-resistant tree species, has significantly lower peak heat release rate (pkHHR), average heat release rate (HRR), average total heat release rate (THR), and calorific value than *Cunninghamia lanceolata* (Xiaoping et al. 2009; Zhou et al. 2009), its combustion temperature is lower and can release more particulate ^{15}N. In the smoke deposition stage of this study, about 40% of the ^{15}N in $PM_{2.5}$ of both *Schima superba* and *Cunninghamia lanceolata* was absorbed by plant leaves. Smoke $PM_{2.5}$ contains inorganic N salts such as NO_3^-, NO_2^-, and NH_3^+, which can penetrate leaves through the cuticle layer (Hu et al. 2019) or enter leaves with particles through stomata (Zhai et al. 2021). Generally speaking, the rougher the leaf surface, the stronger the ability of leaves to retain particles; the larger the stomatal conductance and the stronger the permeability of cuticle layer, the stronger the ability of leaves to absorb N elements; at the same time, due to its water-repellent properties, wax layer on cuticle surface may not be conducive to penetration of N-containing solution (Chávez-García and González-Méndez 2021). Therefore, although *Cunninghamia lanceolata* leaf roughness is about 3 ~ 4 times higher than *Schima superba* and particle retention is greater (Zheng et al. 2022), due to the influence of stomatal conductance and wax layer and cuticle layer permeability on leaf N absorption, it may have led to *Schima superba* and *Cunninghamia lanceolata* having similar ^{15}N migration rates between "$PM_{2.5}$-plant."

N uptake and distribution by plants

In this study, the increase in N content of *Schima superba* and *Cunninghamia lanceolata* was between 5.23 and 11.10%, indicating that the leaf absorption pathway plays a significant role in the growth of plant N content. In previous studies, the increase in plant N content after foliar N application can reach up to 10% (Uscola et al. 2014). To adapt to arid environments, the palisade tissue and spongy tissue cells of most terrestrial plant leaves are mainly distributed near the axial surface and far axial surface, respectively, while stomata mainly exist in spongy tissue cells (far axial surface) with larger intercellular spaces (Rudall and Bateman 2018). In smoke deposition, particles mainly deposit on the near axial surface of leaves; therefore, a large amount of inorganic N salts on the near axial surface are more likely to permeate into the leaves after being dissolved by dew (Eichert and Fernández 2012). At the same time, N can also enter leaves with particles through stomata, but as particle stress increases, stomata gradually close or become blocked (Chen et al. 2017), reducing the passage of particles, thus only a small amount of N can be absorbed by leaves through stomata.

N in plants can be transported bidirectionally through the phloem and xylem (Baslam et al. 2021); therefore, the ^{15}N absorbed by *Schima superba* and *Cunninghamia lanceolata* leaves can be transported to the underground parts via the plant nutrient transport pathway. In this study, the ^{15}N allocation rates of *Schima superba* and *Cunninghamia lanceolata* aboveground parts were significantly higher than those of the belowground parts, which aligns with previous studies (Bowman and Paul 1992; Dong et al. 2002; Uscola et al. 2014) where it was found that the proportions of N absorbed by leaves in the aboveground and belowground parts could reach up to 94 ~ 95% and 5 ~ 6%, respectively. This is due to plants generally prioritizing nutrient supply to leaves to ensure their growth (Tang et al. 2018). However, in this study, the ^{15}N allocation rate of *Cunninghamia lanceolata* belowground parts (31.8 ~ 37.8%) was significantly higher than that of *Schima superba* (7.6 ~ 10.8%), which is related to the difference in root development between the two tree species in this study. In nature, *Cunninghamia lanceolata* roots are usually more developed than *Schima superba*, and the gap between the proportions of roots in the total biomass of the two tree species can reach 2 times (Lidong et al. 2023). As time goes on, the proportion of ^{15}N in the belowground parts of *Schima superba* and *Cunninghamia lanceolata* decreases, while that in the aboveground parts increases, indicating that N in the belowground parts is being transported to the aboveground parts. This is because N is an important component of chlorophyll, protein, enzymes, and other structures in the leaves. When subjected to stress, these structures in leaves are damaged, and N from other parts of plants can be transported to leaves to alleviate the negative impact of stress (Khan et al. 2017; Tang et al. 2018). Simultaneously, when external N supply ceases, it may compel root N to be transported to the leaves. When N absorption in the leaves reaches saturation or N on the leaf surface is leached, N in leaves may be excreted through cuticle layer permeation (Eichert and Fernández 2012).

Stress responses of plants to $PM_{2.5}$ stresses

MDA is a decomposition product of lipid peroxidation after plant cells are damaged by particles, and the level of its content serves as a measure of the extent of particle damage to plant leaves (Alché 2019). Excessive accumulation of MDA can also cause cross-linking and polymerization of proteins, nucleic acids, and other substances, causing them to lose function (Yamauchi et al. 2008). In this study, the MDA content of *Schima superba* and *Cunninghamia lanceolata* increased significantly after being subjected to smoke deposition, which indicates that the absorption of smoke particles inflicted substantial damage on *Schima superba* and *Cunninghamia lanceolata*. Among them, *Schima superba* litter combustion emits more particles, and *Schima superba* leaves are more likely to absorb more $PM_{2.5}$, but *Schima superba* is less damaged by particles, which may be related to the fact that *Schima superba* has more N input. The addition of exogenous N helps to enhance plant antioxidant mechanisms and promote the production of antioxidants (Lal et al. 2023), thereby inhibiting the production of MDA (Li et al. 2020). At the same time, compared with some common subtropical trees, *Schima superba* has been proven to contain more anthocyanins (antioxidants) (Yu et al. 2019), which suggests that *Schima superba* itself might possess a stronger resistance to stress. Overall, although *Cunninghamia lanceolata*'s response to $PM_{2.5}$ invasion is stronger than *Schima superba*, at 1 day, the increase in *Cunninghamia lanceolata* MDA content is not significant, which indicates that *Cunninghamia lanceolata* employs special resistance measures against $PM_{2.5}$ stress during the early stage of smoke deposition. For example, a certain reticular structure can be observed on the surface of *Cunninghamia lanceolata* leaves under a scanning electron microscope, which can slow down the invasion of particles (Zheng et al. 2022). As smoke stress continues (7 ~ 15 days), the increment of MDA content begins to show an upward trend, indicating that particle damage to *Cunninghamia lanceolata* leaves is also deepening.

During smoke deposition, ZA and ABA serve as crucial plant hormones for stress resistance. They play a significant regulatory role in the physiological processes of leaf stress resistance during particulate matter invasion. ZA can prevent the degradation of chlorophyll and protein, maintain cell vitality, etc. (Ali et al. 2022); ABA can protect the biological membrane by inhibiting peroxidation and reducing the accumulation of MDA, regulate the generation of stress-resistant substances (Cao et al. 2020), and also prevent the invasion of particulate matter by inducing stomatal closure (Kuromori et al. 2018). Hence, in this study, it was observed that under $PM_{2.5}$ stress, the content of ZA and ABA in the leaves of *Schima superba* and *Cunninghamia lanceolata* increased to varying degrees when compared to the control group. Among them, the content of ZA and ABA in *Schima superba* has returned to normal levels or has a trend of returning to normal levels within 15 days, while the hormone levels in *Cunninghamia lanceolata* leaves remain at a high level and show no trend of recovery, which is related to the degree of damage to the two tree species. When combined with the MDA content data of *Schima superba* and *Cunninghamia lanceolata*, it can be deduced that *Schima superba*, which sustains a lower degree of damage, releases less ZA and ABA. As the leaves gradually recover, the content of these two hormones also reverts back to normal levels. However, the content of ZA and ABA in *Cunninghamia lanceolata*, which has a higher degree of damage, remains at a high level. Thus, alterations in MDA and stress hormone content suggest that *Schima superba* possesses a stronger ability to cope with smoke stress than *Cunninghamia lanceolata*.

Effects of plant stress on leaf N uptake and accumulation

The attachment of smoke particulate matter can cause leaves to absorb and accumulate a large amount of N, but at the same time, the absorption of particulate matter can have negative effects on the physiological structure and processes of leaves, mainly reflected in the changes in the content of MDA, a product of biological membrane peroxidation reaction, and stress-resistant hormones. Therefore, there may be a certain correlation between the accumulation of N in plant leaves and the content of MDA and endogenous hormones. In *Schima superba*, there was no significant correlation between the accumulation of ^{15}N and the content of MDA, and among plant hormones, it only showed a highly significant positive correlation with the content of ZA. This indicated that when *Schima superba* is subjected to smoke particulate matter stress, it suffers less damage and the accumulation of N in its leaves is almost unaffected. At the same time, the accumulation of N promotes the synthesis of hormones such as ZA (Gautrat et al. 2021), which helps to reduce the damage caused by stress (Kumari et al. 2022). However, numerous studies (Krouk 2016) have also demonstrated a bidirectional influence between the release of plant hormones and the assimilation and transport of N. This means that not only does the accumulation of N in *Schima superba* leaves have a positive effect on the synthesis and release of ZA, but ZA may also have a promoting effect on the accumulation of N. Therefore, there is a positive correlation between the accumulation of N in *Schima superba* leaves and the content of ZA. The significant negative correlation observed between MDA content and 15N accumulation in *Cunninghamia lanceolata* suggests that leaf damage might have inflicted serious negative effects on N accumulation in *Cunninghamia lanceolata*. The more severe the leaf damage, the less N accumulates. At the same time, the transport of N in plants depends on related transport proteins (Huergo et al. 2013), and the accumulation of MDA can also lead to loss of protein function (Traverso et al. 2004), which may inhibit the transport and accumulation of N in plants. It is generally believed that as an important stress-resistant hormone, an increase in ABA content may prevent plant leaf N accumulation from being negatively affected by stress (Vishwakarma et al. 2017). However, in this study, there was a significant negative correlation between ABA content and N accumulation in *Cunninghamia lanceolata*, indicating that it did not promote leaf N accumulation under stress but had an inhibitory effect. This may be because ABA has been shown to inhibit the transport of N from roots to branches and leaves (Liu et al. 2021), so ABA inhibited the transport of N in *Cunninghamia lanceolata* under $PM_{2.5}$ stress. At the same time, $PM_{2.5}$ stress may have accelerated leaf senescence in *Cunninghamia lanceolata*. In senescent leaves of plants, ABA content usually increases (Harrison and Walton 1975), while highly mobile N is transferred from old leaves to other parts of plants, resulting in a decrease in N content in old leaves (Li et al. 2016).

In the actual process of forest fires, conditions such as combustion state (flaming and smoldering), moisture content of combustibles, and type of combustibles have a significant impact on the emission of particulate N, which subsequently influences the “combustible-smoke-leaf-root” migration and absorption process of N elements. During forest fire combustion, the particulate N emission in the smoldering state is higher than in the flaming state. Research indicates that the NH_4^+ emission factor during the smoldering of subtropical forest tree branches and leaves is approximately 1.2 g/kg, significantly higher than flaming (about 0.8 g/kg) (Ma et al. 2019). Variations in the moisture content of combustibles lead to different states of combustion (Zhao et al. 2021), which results in distinct characteristics of particulate N emissions during combustion. The primary manifestation is that an increase in the moisture content of combustibles promotes the emission of particulate N. Studies have shown that when the moisture content of litter in Nevada, USA, increases from 0 to 20%, the NH_4^+ and NO_3^- emission factors increase from 0.04 and 0.05 g/kg to 0.20 and 0.30 g/kg, respectively (Chen et al. 2010). Different types of combustibles possess unique combustion characteristics, which directly lead to variations in emission characteristics among combustibles (Ma et al. 2022). Research indicates that the NH_4^+, NO_3^-, and NO_2^- emission factors of Boreal forest tree branches and leaves are all higher for broad-leaved trees than for coniferous trees (Ma et al. 2019). Additionally, during the smoke deposition process, forest fires could potentially impact the adsorption of particulate N by plant leaves. In forest fires of varying intensities, there are differences in the quantity of smoke particles adsorbed by leaves. Studies have shown that during forest fire smoke stress, as forest fire intensity increases, *Schima superba* leaves significantly increase their adsorption of $PM_{2.5}$ (Zheng et al. 2022).

Conclusion

This study conducted a comprehensive analysis of the pathways and rates of N migration during the release and deposition of $PM_{2.5}$ from forest fire smoke, examined the impacts of $PM_{2.5}$ stress on the content of stress response products in leaves, and explored the correlation between leaf N accumulation and these stress response products. Based on the findings of this research, we can draw the following conclusions.

1 N in combustible materials can be transported to plant leaves via $PM_{2.5}$ particles in smoke during combustion. Once absorbed by the leaves, this N can be distributed and assimilated throughout various parts of the plant. The migration and absorption of N occur in a stepwise decreasing manner over time. As time progresses, the transport of N from the underground parts to the aboveground parts of *Schima superba* and *Cunninghamia lanceolata* increases. Notably, the rate of N migration during smoke release is higher in *Schima superba* than in *Cunninghamia lanceolata*. After N is absorbed by the leaves, a larger proportion of it can be allocated to the underground parts of *Cunninghamia lanceolata*.
2 Both *Schima superba* and *Cunninghamia lanceolata* exhibited stress responses under $PM_{2.5}$ stress, characterized by varying degrees of increase in the content of MDA, ZA, and ABA in the leaves of both tree species. However, the stress response of *Schima superba* was notably less pronounced than that of *Cunninghamia lanceolata*, indicating a stronger recovery ability in *Schima superba*.
3 Under the influence of $PM_{2.5}$ stress, *Schima superba* demonstrated a significant positive correlation between N accumulation and ZA content. This suggests that the absorption of N effectively bolstered the ability of *Schima superba* to resist $PM_{2.5}$ stress. Conversely, in *Cunninghamia lanceolata*, a significant negative correlation was observed between N accumulation and the content of MDA and ABA. This could potentially be attributed to more severe damage sustained by *Cunninghamia lanceolata* under $PM_{2.5}$ stress.

Therefore, to mitigate the impact of forest fire smoke on surrounding ecosystems, it is crucial to prioritize forest fire prevention in China's forestry production process. This could involve reducing the scale and frequency of mountain refining. Simultaneously, as significant fire-resistant and timber tree species in China, *Schima superba* and *Cunninghamia lanceolata* exhibit varying degrees of fire resistance and tolerance to $PM_{2.5}$ smoke stress. To strike a balance between overall fire resistance, smoke tolerance, and economic considerations in forests, it is necessary to plant these two tree species in appropriate proportions during afforestation.

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Authors' contributions
HL proposed the research ideas and methods, participated in the entire process of combustible combustion and smoke simulation sedimentation test, organized and analyzed the test data, and was one of the main contributors to the writing of the manuscript. YM proposed research ideas and methods, guided experiments, sampling, and sample determination; organized and analyzed test data; and was also one of the main contributors to the writing of the manuscript. PZ is responsible for the collection, storage, and determination of combustibles, smoke, and plant samples. ZH conducted combustible combustion and smoke simulation sedimentation tests. XZ carried out debugging and maintenance of test equipment and organized and stored test data. MT guided the writing of the manuscript and reviewed and revised the manuscript. FG proposed research ideas, guided the writing of the manuscript, and reviewed and revised the manuscript. All authors have read and approved the final manuscript.

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Availability of data and materials
All data generated or analyzed during this study are included in this published article [and its supplementary information files].

Declarations

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Not applicable.

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The authors declare that they have no competing interests.

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