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A meta-analysis of elevated O_3 effects on the Photosynthesis of Shrubs

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Abstract. In our research, we collected and compiled 100 sets of publicly available O_3 fumigation experimental observations from the past 35 years (1990 to 2025), which underwent rigorous quality control and use an integrated meta-analysis, we comprehensively examined the response of shrub photosynthesis to O_3, highlighting the effects of O_3 concentration, duration of the experiment, and climate type on this response. The results showed that under elevated O_3 stress, the chlorophyll content (Chl) and net photosynthetic rate (Pn) of shrubs growing in temperate regions decreased the most, by 24.01% and 48.40%. Different O_3 concentrations had significant differences in their impact on the Pn in the shrubs: when the O_3concentration was 81-160 nmol/mol, Pn decreased the least, approximately 24.05%. In the same O_3 environment, the length of stress time had no significant difference on the Pn of shrubs. However, the length of stress time had a highly significant difference in its impact on the Chl content in the shrubs: when the stress time was 8-15 days, the Chl content decreased the most, approximately 39.87%. Our research demonstrated that under elevated O_3 conditions, the duration of stress and the climatic type of the growth region exert a more pronounced influence on chlorophyll (Chl) content, stomatal conductance (Gs), and net photosynthetic rate (Pn) in shrubs. Elevated O_3 has the most substantial effect on the photosynthetic parameters of shrubs located in temperate regions. Future research should focus on the stress impacts of elevated O_3 on temperate shrubs, and strategies to improve the stress resistance of these shrubs in this region should be investigated.

1 Introduction

Influenced by factors including industrial emissions, solvent usage, and agricultural activities, ambient O_3 concentrations during the summer have exhibited an upward trend in 74% of cities globally. The average annual increase is 0.6%, with some cities experiencing rises of up to 3%[1]. The O_3 levels in these cities have exceeded the established plant tolerance threshold of 50 nmol/mol, beyond which plants suffer varying degrees of damage[2]. Research indicates that the sustained increase in O_3 concentrations is a primary factor contributing to forest degradation in Europe, the United States, and other regions[3]. Forest ecosystems in China are facing considerable stress due to elevated O_3. In 2021, the annual 90th percentile of O_3-8h concentration in Jinan City was as high as 90 nmol/mol[4]. In 2022, peak O_3 concentrations in multiple cities across the Beijing-Tianjin-Hebei region reached 92 nmol/mol[5]. Therefore, high surface-level O_3 has emerged as one of the primary atmospheric pollutants in China during 2020-2025, exerting substantial pressure on forest ecosystems.

Compared to herbaceous plants, shrubs demonstrate enhanced carbon sequestration, superior photosynthetic efficiency, and more effective ecological restoration capabilities. Research indicates that shrub can lower wind speed by 40%[6], while also contributing significantly to biodiversity conservation and the acceleration of natural vegetation recovery. Elevated O_3 concentrations can damage shrub leaves and inhibit photosynthesis. Research indicates that elevated O_3 induce yellow-brown or greenish-yellow spots on the leaf surfaces of Lonicera japonica shrubs, leading to membrane lipid peroxidation. Consequently, the content of malondialdehyde (MDA), a marker of membrane lipid peroxidation, increases by 11.2%~50.0%[2,7]. Additionally, studies on Lonicera japonica have demonstrated that exposure to elevated O_3 results in the net photosynthetic rate (Pn) declines by 44.0%~51.5%[8-9]. Currently, there is a paucity of relevant studies on shrubs, which primarily concentrate on the alterations in specific photosynthetic indices of plants belonging to a single family or a particular common species in environments with elevated O_3 concentrations. However, investigations into the impacts of elevated O_3 pollution on shrubs belonging to diverse families within a unified experimental framework have been scarce. Consequently, a comprehensive exploration of the variations in key parameters related to shrub photosynthesis under heightened O_3 stress is crucial for safeguarding the ecological balance and enhancing plant resilience.

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In our research, we analyzed data from published research conducted between 1990 and 2025 and synthesized extensive datasets from relatively independent studies through meta-analysis. Our objectives were to explore: (1) the range of fluctuations in shrub photosynthetic metrics, including chlorophyll content (Chl), net photosynthetic rate (Pn), and stomatal conductance (Gs), under varying O_3 concentrations; (2) the changes in these photosynthetic metrics of shrubs over the course of the experimental duration; (3) the differences in their photosynthetic responses to increasing O_3 concentrations across different climatic zones. Ultimately, we assessed the effects of elevated O_3 concentrations on shrub photosynthesis by considering O_3 levels, the duration of experiments, and climate type. This analysis aims to provide a foundation for investigating ecosystem protection in the context of global climate change.

2 Materials and Methods

2.1 Data Sources

Data for this study were collected from peer-reviewed publications obtained from the China National Knowledge Infrastructure (CNKI) and the Web of Science (WOS), encompassing the period from 1990 to 2025. A literature search was performed using the keywords: "ozone or O_3," "plant or botany," "blade," and "photosynthetical system" within the CNKI and WOS databases. The initial search yielded a total of 7591 publications. Following a title screening, 1034 publications from CNKI and 1,491 from WOS were selected for further evaluation. To further determine whether research reports was included in the meta-analysis, we adopted the following screening criteria: (1)the study focused on shrubs; (2) photosynthetic parameters included Chl, Pn, Gs and intercellular CO_2 concentration (Ci); (3) the experiment incorporated an elevated O_3 treatment alongside an ambient O_3 control (CK) group, with O_3 concentrations in the treatment group $\geq$ 40 nmol/mol; (4) the duration of O_3 exposure exceeded one day; and (5) the experiment included at least three replications, with mean values accompanied by standard deviation (SD) or standard error (SE). After screening, 15 publications (7 from WOS and 8 from CNKI) met all criteria, providing data from 19 experimental sites (Figure 1, mapped using ArcGIS 10.8). A total of 100 subgroup datasets for Chl, Pn, and, Gs along with 4 overall effect datasets for Ci, were included in the meta-analysis.

Raw data were collected from the textual content, tables, and figures of published research. For each target variable, data included the mean values, standard deviation (SD), and number of replications (n) for both the control group and the treatment group. In cases where data were presented as graphs, they were extracted using GetData Graph Digitizer V2.25 software. If only the standard error (SE) was provided in the literature, SD was converted from SE using Equation (1):

$$SD=SE\times\sqrt{N} \tag{1}$$

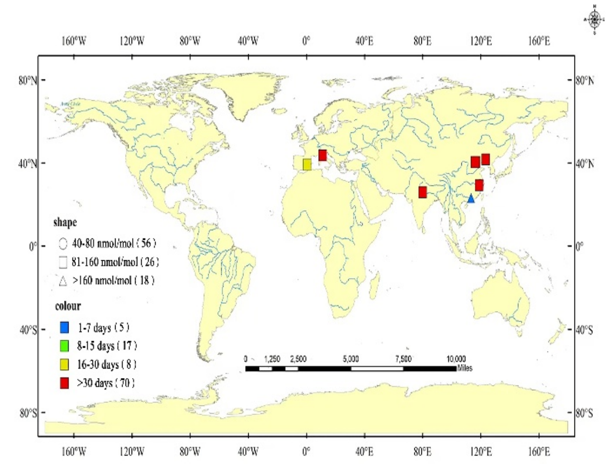

Figure 1. Study the global distribution map of sample sites

2.2 Data Classification

The stress effects of elevated O_3 on shrub photosynthetic indices are influenced by multiple factors, which were grouped and classified according to different criteria (Table 1). Specifically, the O_3 concentration was divided into three levels: 40-80 nmol/mol, 81-160 nmol/mol, and >160 nmol/mol. The stress duration was categorized into four groups: 1-7 days, 8-15 days, 16-30 days, and more than 30 days. Shrubs were classified based on the climatic types of their growing regions, including temperate, subtropical, and tropical zones.

Table 1. Classification of influencing factors variables

Categorical variable	Level 1	Level 2	Level 3	Level 4
O_3 concentration (nmol/mol)	40-80	81-160	>160	
Experiment duration (days)	1-7	8-15	16-30	>30
climate type	temperate zone	subtropical zone	torrid zone	

2.3 Meta-Analysis

The meta-analysis in this study was conducted following the procedure proposed by Hedges et al. (1999)[10]. Effect size was used as a quantitative indicator to characterize the strength of the effects induced by elevated O_3 concentrations relative to the control (CK) group[11]. The effect sizes for parameters such as Chl, Pn, Gs, and Ci, were the natural logarithms of the response ratio (RR)[12], and the specific calculation formula is as follows:

$$lnRR=ln\frac{X_t}{X_c} \tag{2}$$

The effect size is denoted by lnRR, with X_t and X_c representing the mean values of the elevated O_3 treatment and CK groups, respectively.

The variance (V) for each independent study was calculated as follows:

$$V=\frac{SD_t^2}{N_t X_t^2}+\frac{SD_c^2}{N_c X_c^2} \quad (3)$$

Here, SD_t and SD_c are the standard deviations of the O_3 treatment group and the CK group, while N_t and N_c are the sample sizes of the O_3 treatment group and the CK group.

The random-effects model in Metawin 2.1 software was employed to calculate the 95% confidence intervals of the weighted response ratios[13].

The impact of elevated O_3 concentration on shrub photosynthetic parameters was expressed as a percentage, calculated as follows:

$$\text{change}(\%)=(e^{RR_{++}}-1)\times 100\% \quad (4)$$

A positive calculation result indicates that elevated O_3 concentration has a positive effect on photosynthetic parameters compared to the control group, while a negative result indicates a negative effect. If the 95% confidence intervals (95% CI) does not overlap with 0, it is considered to have a significant difference (P<0.05)[14]. If the 95% CIs of effect sizes at different levels within the same group in subgroup analysis overlap, it indicates no significant difference.

Prior to combining the effect sizes from each independent study to calculate the mean effect size, a chi-square test was employed to assess data heterogeneity, with degrees of freedom set at (n-1). In the absence of significant heterogeneity (P>0.05), the fixed-effects model was adopted. When significant heterogeneity was detected (P<0.05), the random-effects model was employed instead. To explore whether variations in O_3 concentration, fumigation duration, and the climatic type of the experimental site could lead to differences in the impact of O_3 on shrub photosynthetic parameters, the total heterogeneity (Q_T) was partitioned into within-group heterogeneity (Q_W) and between-group heterogeneity (Q_B). A significant difference in the mean effect size across categorical groups was considered present when the P values for Q_B was less than 0.05 (P<0.05), suggesting that this particular grouping exerts a significant influence on the corresponding photosynthetic parameters. The results of the heterogeneity tests conducted in this study are presented in Table 2 and Table 3.

Table 2. Total heterogeneity (Q_T) and Rosenthal's Methods test results

influence factor	Observation number	Q_{total}	P	Rosenthal's Methods
Chl	40	60.03	*P<0.05*	386.2
Pn	30	71.94	*P<0.05*	1306.4
Gs	30	26.77	*P=0.58*	202.5
Ci	4	2.59	*P=0.46*	187.5

Note: Chl represents chlorophyll content, Pn represents net photosynthetic rate, Gs represents stomatal conductance, Ci represents intercellular CO_2 concentrationand A value of P < 0.05 signifies a significant effect, while P < 0.01 indicates an extremely significant effect.

Table 3. Classification total heterogeneity (Q_T), inter-group property (Q_B) and intra-group heterogeneity (Q_W) were tested

influence factor	sectionalization	Q_T	Q_W	Q_B
Chl	L_1	55.05	50.23	4.82
	L_2	63.93	48.21	15.71
	L_3	73.75	66.60	7.14
Pn	L_1	98.36	92.21	6.15
	L_2	98.24	96.95	1.29
	L_3	266.62	77.76	188.86
Gs	L_1	24.58	21.99	2.59
	L_2	23.46	22.06	1.40
	L_3	28.43	24.96	3.48

Meta-analysis is a systematic research approach built upon individual independent studies. When conducting a meta-analysis, it is crucial to pay attention to the issue of publication bias. In this study, Rosenthal's Methods, specifically the fail-safe number (Nfs) approach, was employed to test for publication bias in the collected data. The threshold for the fail-safe number is calculated as (5n+10), where n represents the amount of data collected in the meta-analysis. When the fail-safe number of the meta-analysis data is lower than this threshold, it indicates the presence of publication bias in the study, and accurate results cannot be obtained through the meta-analysis. In this research, the fail-safe numbers for Chl, Pn, Gs, and Ci are all significantly higher than the fail-safe number threshold (as shown in Table 2). Therefore, there is no publication bias.

To compile literature data for database construction, we utilized Microsoft Excel 2016, followed by basic statistical calculations. The analysis was conducted using MetaWin 2.1 software, where the mean effect value was calculated employing the random effects model bootstrap method. Additionally, the significance of factors influencing the physiological and ecological indicators of shrubs was assessed using the random forest method in the R programming language[15], The graphing software employed was Origin 2022.

3 Results

3.1 Effects of Elevated O_3 on photosynthetic indices of shrubs

Elevated O_3 exerted significant effects on Chl 、Pn and Gs in shrubs (P< 0.05), resulting in decreases of 16.70% (-23.56%~ -9.59%)、31.78% (-39.25% ~ -0.24%) and 22.25% (-29.99%~-14.23%) (Figures 2a, b, c). However, elevated O_3 stress showed no significant effect on Ci in shrubs (Figure 2d).

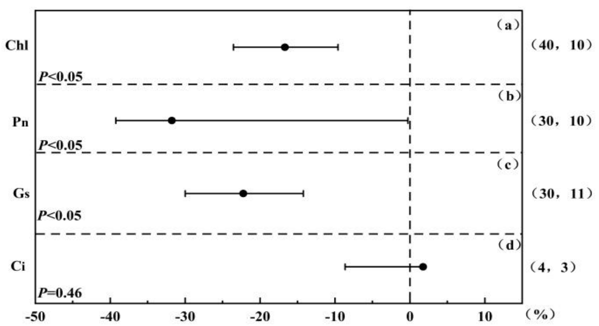

Figure 2. Effects of O_3 concentration on photosynthetic indices of shrubs

3.2 Effects of elevated O_3 on photosynthetic pigment content in shrubs

The elevated O_3 levels led to a decrease in Chl content in the shrubs (Fig. 3). The analysis revealed no significant differences among the three treatment concentrations. Focusing on the four groups representing different stress durations, the results revealed highly significant differences among the groups concerning the various stress times ($P<0.01$): the most substantial decrease in Chl content occurred after 8-15 days of stress, amounting to approximately 39.87%. Analysis of the different climatic zones revealed that shrubs in temperate regions experienced the most significant reduction in Chl content under high O_3 concentrations, with a decrease of about 24.01%. In contrast, shrubs in subtropical and tropical regions experienced reductions of 17% and 6.27%.

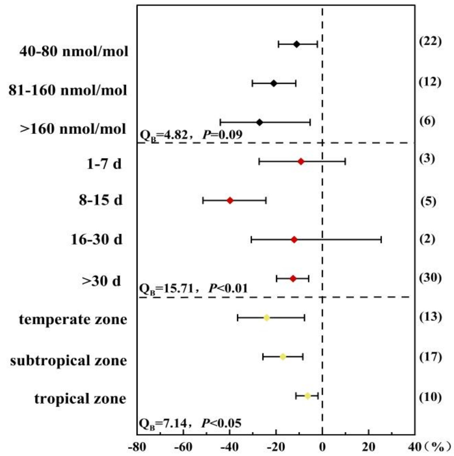

Figure 3. Effects of elevated O_3 on photosynthetic pigment content in shrubs

3.3 Effects of elevated O_3 on Gas Exchange Responses in shrubs

The elevated O_3 inhibited both Pn and Gs (Figs. 4a and 4b). Analysis of Pn changes under high O_3 stress revealed significant differences ($P< 0.05$) among various O_3 concentration treatments. The most substantial decrease in Pn occurred when the O_3 concentration exceeded 160 nmol/mol, resulting in a 35.83% reduction. When examining differences among the three climate types, results indicated a highly significant difference ($P < 0.01$): shrubs in the temperate zone exhibited the greatest reduction in Pn, approximately 48.40%, while shrubs in the subtropics and tropics experienced decreases of 6.69% and 20.98%, respectively. No significant within-group differences were observed among treatments at varying stress durations. Furthermore, analysis of Gs changes under elevated O_3 indicated that the within-group differences among different O_3 concentration treatments, stress duration treatments, and climate types were not significant.

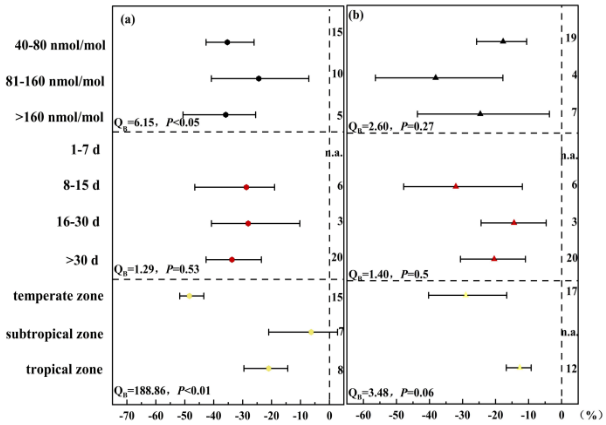

Figure 4. Effects of elevated O_3 on Gas Exchange Responses in shrubs

3.4 Importance of Various Factors on Target Variables in the Shrub Photosynthetic System

The outcomes of the random forest modeling analysis revealed that stress duration and shrub growth climate significantly influenced Chl content, while the impact of O_3 concentration on Chl content variability was minor and lacked predictive capability in the current study conditions (Fig. 5a). Stress duration and shrub growth climate were identified as primary factors driving Pn, with stress duration exerting a notably significant influence (Fig. 5b). Additionally, stress timing and climatic conditions of shrub emerged as crucial determinants of Gs (Fig. 5c).

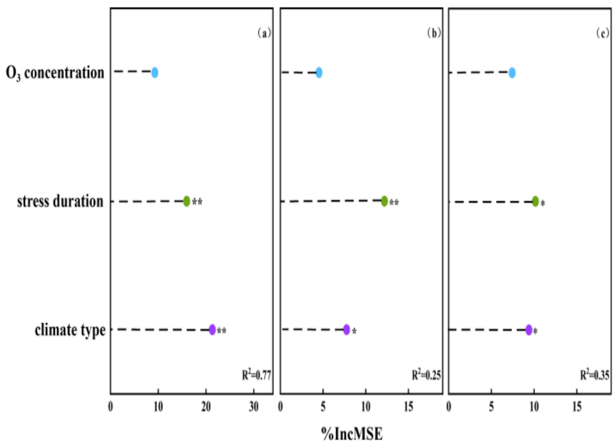

Figure 5. Relative importance (%IncMSE) of explanatory factors in photosynthetic pigment content and photosynthetic gas exchange parameters responses to elevated O_3

Note:(a) Chl, (b) Pn, and (c)Gs. $P<0.05$ means significant, * means $P<0.05$, ** means $P<0.01$

4 Discussion

4.1 Effects of Different Ambient O_3 Concentrations on the Shrub Photosynthetic System

In our research, with the continuous increase of O_3 concentration, the photosynthetic indices of shrubs showed varying degrees of decrease. When the O_3 concentration exceeded 160 nmol/mol, the reductions in Chl content and Pn in shrubs were most pronounced. This phenomenon can be attributed to the impairment of photosynthetic structures on the thylakoid membranes of plant chloroplasts under elevated O_3 stress[16], leading to a reduction in leaf Chl content. As O_3 concentration increases, the plant antioxidant system is progressively impaired, thereby inhibiting Chl biosynthesis[17]. As a key photosynthetic pigment, Chl is essential for light absorption and energy transfer[18]. A reduction in Chl content diminishes both light and dark reaction rates, decreases light-harvesting efficiency, and consequently leads to a decline in Pn[19].

When shrubs were exposed to an O_3 concentration of 81-160 nmol/mol, the Gs showed the greatest reduction (approximately 40%), while the decrease in Pn was the smallest (approximately 25%). The reasons are as follows: with the intensification of O_3 pollution, the ambient O_3 concentration in many regions during summer has approached 60-70 nmol/mol[20], enabling plants to develop a certain degree of adaptability. Therefore, when the O_3 concentration reaches 80 nmol/mol, shrub leaves maintain normal gas exchange activities, leading to no significant change in Gs. However, as the O_3 concentration increases further, the leaf regulation mechanism in shrubs is activated, resulting in stomatal closure and a subsequent decrease in Gs[21]. When the O_3 concentration surpasses 160 nmol/mol, the antioxidant system in shrubs becomes compromised[22], resulting in diminished stomatal regulation capacity and an increase in Gs. As a result, the most significant reduction in Gs occurs when shrubs are subjected to an O_3 concentration ranging from 81-160 nmol/mol. The minimal reduction in Pn at this concentration may be ascribed to the activation of the antioxidant regulatory system in shrubs under heightened O_3 stress, which aids in the recovery of plant photosynthesis[23].

4.2 Effects of Stress Duration on the Shrub Photosynthetic System Under Elevated O_3 Stress

Compared to other stress durations, both Chl and Gs were most significantly reduced in shrubs during the 8-15 days stress period. This reduction occurred because, at the onset of O_3 exposure, the shrubs faced high concentrations of O_3, which damaged the chloroplast structure. Consequently, this damage led to a decline in the photosynthetic capacity of the chloroplasts and a decrease in the levels of photosynthetic pigments[24]. When O_3 enters shrub leaves, it generates reactive oxygen species (ROS), which exacerbate the lipid peroxidation of shrub cell membranes and further affect stomatal movement, resulting in a decrease in Gs[25]. When Gs decreases due to elevated ambient O_3 concentration, CO_2 entry is hindered, while the existing CO_2 in cells is still consumed during photosynthesis, leading to a decrease in Ci. This result is consistent with the research by Guo Chenglong et al.[26].

Chl content and Gs decreased to a lesser extent in shrubs experiencing prolonged stress (exposed to high O_3 stress for over 15 days).This phenomenon is attributed to the shrubs' compensatory mechanisms, where high ozone levels trigger their antioxidant system, leading to a temporary rise in Chl content[27]. In addition, environmental factors such as temperature, light, and humidity in the experiment may have a certain impact on elevated O_3 stress. When plants are in an environment with suitable light and temperature, their photosynthesis is stronger, which can provide more energy and substances for Chl synthesis, helping to maintain Chl content[28]. With the extension of elevated O_3 stress duration, the self-regulation ability of shrubs improves, and the protective enzyme system begins to function. Shrubs can adjust the turgor pressure regulation mechanism of stomatal guard cells to gradually adapt to the stress environment, slowing down the decreasing trend of Gs to maintain a certain level of gas exchange and photosynthesis.

4.3 Effects of different climate types on the Shrub Photosynthetic System Under Elevated O_3 Stress

Elevated O_3 had a more pronounced impact on the photosynthetic system of shrubs in the temperate zone compared to those in other climatic regions. In temperate shrubs, Chl, Gs, and Pn were significantly reduced, exceeding the reductions observed in shrubs located in subtropical and tropical zones. This disparity may be attributed to the generally higher Gs observed in shrubs from subtropical and tropical climates; When plants are exposed to elevated O_3 stress, plants rapidly regulate stomatal aperture in response to elevated O_3 stress, and this physiological process is modulated by external factors including light and temperature[29]. Compared with the large diurnal temperature difference in some temperate regions, subtropical and tropical regions provide more suitable temperature conditions for plants[30], the longer light duration in tropical regions requires shrubs to produce more Chl to capture light energy. Therefore, the Chl content, Gs, and Pn of shrubs grown in tropical and subtropical regions are generally higher than those grown in temperate regions.In addition, the main types of trees growing in different climatic zones are different. Evergreen Broad-leaved Shrubs are predominantly distributed across tropical and subtropical regions[31]; compared with shrubs in temperate regions, they may have higher stomatal density and longer opening time, resulting in greater damage to temperate shrubs.

In our research, we comprehensively summarized the research results on the effects of global elevated O_3 environment on shrubs up to 2025. Although only 15 studies were included (a relatively small number), previous studies have confirmed that such a sample size can meet the requirements of meta-analysis[32]. However, due to the limitations of research data, we mainly analyzed the effects of elevated O_3 environment on shrub photosynthetic pigments, Pn, Gs, and other indices. Ci could not be subjected to subgroup analysis due to the limited number of studies, making it impossible to determine its main influencing factors. In future research, we should pay more attention to the effects of elevated O_3 environment on other photosynthetic indices such as Ci, and further explore the mechanism by which elevated O_3 concentration affects the shrub photosynthetic system.

5 Conclusion

This study synthesizes global research published through 2025 regarding shrub responses to elevated O_3 exposure. The key outcomes are summarized as follows. (1) O_3 stress duration and regional climate type both significantly altered shrub Chl content *($P<0.05$)*. Temperate shrub species showed the largest Chl decline, averaging a 24.01% reduction. (2) O_3 exposure length and growing-region climate served as dominant regulators of shrub Chl content, Gs, and Pn. (3) There are significant differences in the impacts of the climatic type of the shrub growth region and different O_3 concentrations on the Pn of shrubs. Shrubs growing in temperate zones show the most pronounced decline in Pn, with an approximate reduction of 48.40%. Nonetheless, current data constraints limit the present analysis to O_3-driven changes in shrub photosynthetic function. How elevated near-surface O_3 reshapes shrub antioxidant metabolism remains poorly documented and warrants targeted investigation in future work.

Acknowledgments

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