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ORIGINAL ARTICLE

Soil nitrogen availability determines the CO_2 fertilization effect on tree species (*Neolamarckia cadamba*): growth and physiological evidence

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Abstract

Urban plantation species experience multiple stresses. Among these, the two significant challenges are increasing atmospheric CO_2 concentration and nutrient-depleted soils, which significantly impede growth, development, as well as the adaptation and mitigation capacity of plant species. This study hypothesized whether nitrogen availability improves CO_2 fertilization effects and the growth of urban plantation tree species (*Neolamarckia cadamba*) under rising atmospheric CO_2 concentration.The plants were grown in nitrogen regimes (low-N_{200} Kg N ha^{-1}, medium-N_{300} Kg N ha^{-1}, and high-N_{500} Kg N ha^{-1}) under elevated CO_2 concentration (eCO_2; 800 ± 20 μmolCO_2 mol^{-1}) and ambient conditions ($aCO_{2;}$ 400 ± 14 μmolCO_2 mol^{-1}). We reported that growth and physiological traits were significantly improved under elevated CO_2 concentration and applied nitrogen compared to low nitrogen and ambient CO_2 concentration. The height, stem diameter, leaves, leaf area, and branches were increased by 25%, 13%, 12%, 6%, and 21%, respectively, under N_{300} and eCO_2 than counterparts. The leaf CO_2 assimilation, transpiration, and stomatal conductance were enhanced by 17%, 39%, and 57%, respectively, whereas water use efficiency declined under N_{300} and eCO_2 but slightly increased in eCO_2 and N_{500}. We inferred that nitrogen management practices would improve the benefits of rising atmospheric CO_2 concentration, resulting in improved plant growth and development and better adaptive physiological response and mitigation potential of plantation species.

Keywords Carbon sequestration · Elevated CO_2 concentration · *Neolamarckia cadamba* · Soil nitrogen · Tree growth · Urban tree physiology · Urban resilience

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Introduction

Carbon dioxide (CO_2) is enriched in the atmosphere due to anthropogenic activities, mainly the burning of fossil fuels, deforestation, industrial processes, changing lifestyles, etc., leading to global climate change (Singh and Kumar 2022). Atmospheric CO_2 concentration has increased since the pre-industrial era, which is expected to reach 720-1000 ppm and will contribute to a rise in global air temperatures from 2.6 to 5.4°C by the end of the 21st century (Sharma et al. 2021).The rise in atmospheric CO_2 concentration is anticipated to influence the vegetation system's structure, function, and overall productivity (Prakash et al. 2022).

Elevated atmospheric CO_2 generally enhances plant growth by stimulating photosynthesis mechanisms (Singh et al. 2018). This phenomenon leads to improved biomass production and higher yields, especially when sufficient resources such as soil nitrogen (N), water, and favorable temperatures are available (Chen et al. 2019; Dhyani et al. 2021; Kumar et al. 2021). Nevertheless, in the face of changing climatic conditions, studies indicated that soil nitrogen may be depleted due to higher plant growth rates under rising atmospheric CO_2 concentrations (Stitt and Krapp 1999; Xu et al. 2022). The scenario of diminishing soil nitrogen under changing climatic conditions may result in reduced CO_2 fertilization effects (Stitt and Krapp 1999; Yadav et al. 2019a, b; Nirmal et al. 2021). Hence, supplementing reactive nitrogen to the soil system is essential in such a scenario to meet the plant nitrogen requirements, ensuring optimal plant growth, development, and carbon sequestration (Singh et al. 2014).

Low soil nitrogen affects tree nitrogen levels, including proteins and enzymes that can alter metabolic mechanisms, including physiological processes (Singh et al. 2014; Liu et al.2018; Liao et al. 2019; Ata-Ul-Karim et al. 2022; Xu et al. 2022). Moreover, nitrogen deficient soil alters the tree phenology and insects, including pollinators, thereby disrupting the entire forest system/ecosystem (Huang et al. 2018; Wang and Tang 2019; Ata-Ul -Karim et al. 2022). Liu et al. (2018) reported increased plant biomass by 30.77% and 31.37% at low (4 mg/L) and high (6 mg/L) application, respectively, under elevated CO_2 conditions (700 μmol mol^{-1}). Xu et al. (2022) found that elevated CO_2 (800 ± 20 μmol mol^{-1}) in conjunction with nitrogen application strongly increased shoot and root biomass and the nitrogen and protein concentrations of *Agropyron mongolicum*. Stitt and Krapp (1999) reported that plants growing in a CO_2-enriched atmosphere require higher nitrogen fertilizers for proper physiological function and other metabolic processes. Wei et al. (2018) found higher tomato yields with improved quality, increased CO_2 concentration, and higher nitrogen application to maintain tomato yield and quality in the future with changing climate scenario.

Therefore, soil deficiency in climate change scenarios would profoundly impact various tree species, particularly in non-agricultural settings, such as urban plantations, roadside plantings, and similar environments where nitrogen application is not a common practice.(Gómez-Guerrero and Doane 2018). This phenomenon may significantly diminish urban trees' CO_2 absorption potential and productivity, resulting in a decline in tree species' adaptation and mitigation potential. This scenario may be a major problem in urban areas where limited resources and elevated atmospheric CO_2, temperature, air pollutants, etc, are now becoming common (Singh et al. 2018; Sharma et al. 2018; Sharma and Singh 2021).

In regions like India, where effective nutrient management practices in plantation forestry are not widely implemented, challenges such as limited soil nitrogen availability and changing climatic conditions would substantially impact the productivity of tree species. Under these circumstances, the ability to adapt to and effectively mitigate the consequences of climate change through the forestry system becomes increasingly challenging. Hence, there is a pressing need to enhance the mitigation potential of forestry and tree species in terms of carbon sequestration. This could serve as a potent mechanism to counteract global climate change through strategic forestry interventions.Optimization of nitrogen use presents a valuable approach to enhance the carbon sequestration rate and productivity in nitrogen-deprived soils. Species-specific application of nitrogen to the soil system may effectively boost tree species' carbon sequestration capacity, contributing towards achieving Sustainable Development Goals' targets via adapting and mitigating climate change by forestry system.There is a lack of scientific understanding regarding the influence of soil nitrogen availability on the growth, development, and physiological response of tree species under elevated CO_2 concentrations. Therefore, the present study aims to elucidate the effects of nitrogen applications on the biophysical, growth, and physiological responses of *Neolamarckia cadamba* grown under elevated CO_2 concentration.

Material and methods

Experimental setup

The study was conducted in the automated open chambers (OTCs) facility existing at the Forest Research Institute, Dehradun, Uttarakhand (32°20′ 44.2172″ N, 78°0′ 41.6185″ E, and 668 m.a.s.l.). This system consists of three components, namely open-top chambers (OTCs), CO_2 distribution system, and the controller with the data logger. The size of each OTC was 3.0 × 3.0 ×4.0 m (width × length × height).

The experiment was set up in a split-plot design with three replications of nitrogen and CO_2 concentration. A set of three-month-old and uniform seedlings (n=6 seedlings) of *N. cadamba* were exposed to ambient CO_2 concentration ($aCO_{2;}$ 400 ± 14 μmol CO_2 mol^{-1}) and elevated CO_2 concentration (eCO_2, 800 ± 20 μmol mol^{-1}) in automated OTCs conditions. In addition, the potted seedlings were supplied with three nitrogen regimes (Low nitrogen-N_{200} kg N ha^{-1}, medium nitrogen-N_{300} kg N ha^{-1}, and high nitrogen-N_{500} kg N ha^{-1}) under the above conditions. CO_2 concentration and nitrogen application were considered the main and subplot treatments, respectively.

Analysis of biophysical and growth traits

Biophysical and growth traits, mainly plant height (cm), collar diameter (mm), leaves, branches, and leaf area (cm^2 $leaf^{-1}$) were measured from the plants growing in the treatments. Plant height and collar diameter were measured using a meter scale and digital vernier calliper, respectively (Sharma et al. 2018). Leaf area was computed using the graph paper method (Singh et al. 2018). Leaves were detached carefully from the plants and spread over the graph paper (millimeter scale). The area of the graph paper covered with leaves was then counted to estimate the leaf area per leaf (Singh et al. 2018).

Analysis of physiological functional traits

The response of physiological functional traits determines plant species' performance, adaptation, and productivity were measured. The critical physiological functional characteristics such as CO_2 assimilation rate (*A*, μmol CO_2 m^{-2} s^{-1}), transpiration rate (*E*, mmol H_2O m^{-2} s^{-1}), stomatal conductance (G*s*, mol H_2O m^{-2} s^{-1}), and water use efficiency (WUE) were investigated using portable photosynthetic system (Model 6400 XT- LICOR, Incl, USA) (Singh et al. 2010). The three youngest and fully expanded leaves from each plant were selected to monitor physiological functional traits. Hence, eighteen leaves (n=18) from a set of six seedlings were monitored for physiological parameters in each treatment. All these traits were observed between 11:30 a.m. and 12:30 p.m. under clear skies to avoid the photoinhibition effects. Water use efficiency (WUE) was calculated as the ratio of CO_2 assimilation (*A*) and transpiration (*E*) of the leaf (Singh et al. 2018).

Statistical analysis

The experiment was set up in a split plot design with three replicates. The biophysical, growth, and physiological traits were subjected to ANOVA (=0.05) using STATISTICA 7.0 software to understand the effects of treatments on the plant traits. ANOVA (á=0.05) was used to understand whether the treatment means differed significantly. Pearson correlation was performed with R-Studio software to understand the relationship between the selected tree species' biophysical, growth, and physiological functional traits.

Results and discussion

Response of biophysical and growth traits of plant species

The response of the biophysical and growth traits of the *N. cadamba* plant with increasing atmospheric CO_2 concentration and nitrogen regimes is shown in Figs. 1 and 2. The study showed a significant increase in plant height grown at medium nitrogen availability (N_{300}) compared to low (N_{200}) and high nitrogen levels (N_{500}) under aCO_2 and eCO_2 (Fig. 1). With all nitrogen and CO_2 treatments, the plants grown in medium nitrogen (N_{300}) and eCO_2 (800 ± 20 mol mol^{-1}) showed maximum plant height (189.16 ± 2.63 cm) than medium nitrogen (N_{300}) under aCO_2 (151.41 ± 2.02 cm). This increase in plant height was approximately 25% more than the counterparts (Fig. 1). A carbon dioxide-enriched environment and soil nitrogen availability may synergistically affect plant growth, development, and productivity. Sufficient availability of critical resources such as CO_2 and nitrogen work synergistically and significantly enhance the photosynthesis mechanism, resulting in more carbohydrate and biomass production than either factor alone. Wei et al (2018) found that available soil N mediates the growth and development of tree species in response to increasing atmospheric CO_2 concentration. Further, *N. cadamba* growth was found to be decreased under nitrogen-poor soils (Lu et al. 2021).

The higher collar diameter was reported at medium soil nitrogen (N_{300}) compared to low (N_{200}) and high nitrogen (N_{500}) (Fig. 1). However, collar diameter declined under high nitrogen (N_{500}) with eCO_2 (19.22 ± 1.37 mm). The plant attained higher collar diameter in medium nitrogen (N_{300}) under eCO_2 (26.16 ± 0.75 mm) than aCO_2 (9.57 ± 0.52 mm). This suggested that limited nitrogen availability might impede plant growth under changing climatic variability, particularly under future atmospheric CO_2 concentrations (Medina 2022).

The plants produced more leaves (29.57 ± 2.25) under eCO_2 and medium nitrogen (N_{300}) than aCO_2 (26.42 ± 3.12) (Fig. 1). Further, plants grown in eCO_2 with N_{500} demonstrated less leaves (20.42 ± 0.31) compared to low (N_{200} Kg N ha^{-1}) and medium nitrogen availability (N_{300} Kg N ha^{-1}). Wei et al. (2018) reported soil N depletion due to higher plant growth rates under elevated CO_2 concentration. In such circumstances, nitrogen fertilizers have been applied

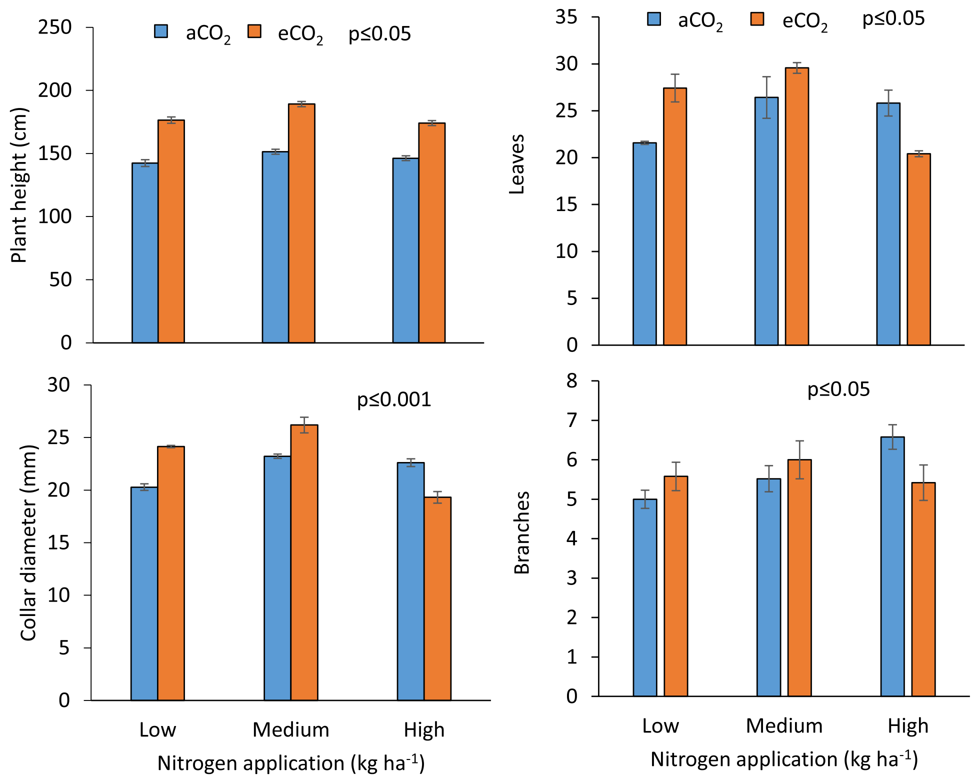

Fig. 1 Effect of nitrogen application (low-N_{200} Kg N ha^{-1}, medium-N_{300} Kg N ha^{-1}, and high-N_{500} Kg N ha^{-1}) on biophysical and growth traits of *N. cadamba* grown under CO_2 concentration (Ambient (aCO_2), 400 ± 14 µmol CO_2 mol^{-1}; Elevated (eCO_2); 800 ± 20 µmol CO_2 mol^{-1}). Error bars indicate the standard error of the mean. Results are mean of six replications (N=6)

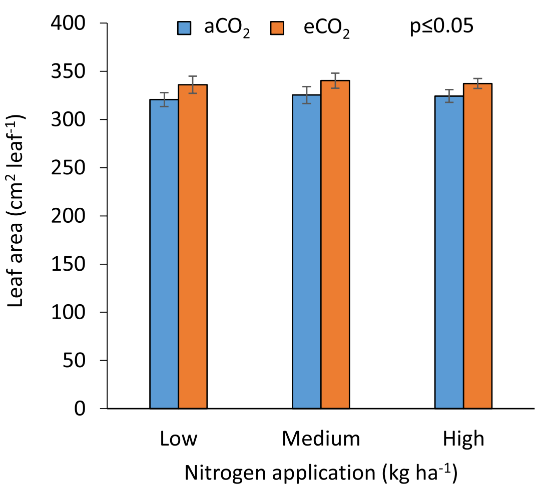

Fig. 2 Effect of nitrogen application (Low-N_{200} Kg N ha^{-1}, medium-N_{300} Kg N ha^{-1}, and high-N_{500} Kg N ha^{-1}) on leaf area of *N. cadamba* grown under CO_2 concentration (Ambient (aCO_2), 400 ± 14 µmol CO_2 mol^{-1}; Elevated (eCO_2); 800 ± 20 µmol CO_2 mol^{-1}). Error bars indicate the standard error of the mean. Results are mean of six replications (N=6)

additionally to take advantage of rising CO_2 concentration to improve the CO_2 fertilization effect (Chen et al. 2019).

Branches per plant were found to be more in N_{300} and N_{500} than N_{200} nitrogen, with the maximum branches (6.58 ± 0.32) at N_{500} under aCO_2 (Fig. 1). Higher leaf area (340.30 ± 7.81 cm^2 $leaf^{-1}$) was at medium nitrogen (N_{300}) under eCO_2 than aCO_2 (325 ± 8.38 cm^2 $leaf^{-1}$) (Fig. 2). The lower soil available N in the face of climate change declines the plant nitrogen content and protein and, in turn, affects the activities of various enzymes involved in the photosynthesis mechanisms, which is the crucial process that decides plant growth performance (Sharma et al. 2017). It has been reported that soil nitrogen availability is the critical constraint of plant growth and development and obtaining beneficial impacts of CO_2-enriched environmental conditions (Schleppi et al. 2019). Hence, understanding how elevated CO_2 and nitrogen affect plant growth dynamics and productivity is essential for accurately predicting the impacts of climate change on the growth dynamics and productivity of tree species at the individual or ecosystem level.

The morphological and physiological function is regulated by nitrogen availability. Nitrogen enrichment promotes plant fitness, tissue nutrition, and shoots and root growth under increased carbon dioxide levels. Increased carbon dioxide and nitrogen interact synergistically to affect plant performance, particularly in relation to plant size, showing that nitrogen effects can be aggregated by increased carbon dioxide (Apurva et al. 2017; Kumari and Singh 2018; Guo et al. 2022). Cao et al. (2008) discovered that an excessive application of nitrogen can have a contrary effect, potentially resulting in a decline in growth and adversely impacting both plant morphology and developmental processes.

Response of physiological functional traits of plant species

The physiological response of *N. cadamba* was significantly affected by increased atmospheric CO_2 concentration and nitrogen regime (Fig. 3). Leaf CO_2 assimilation rate was significantly improved under eCO_2 with medium nitrogen (N_{300}) compared to low (N_{200}) and high nitrogen (N_{500}). Leaf CO_2 assimilation rate was highest (9.00 ± 0.42 µmol CO_2 m^{-2} s^{-1}) and increased by 16% in N_{300} and eCO_2 than aCO_2 (7.73 ± 0.33 µmol CO_2 m^{-2} s^{-1}) (Fig 3). Riberio et al. (2021) reported an enhanced leaf CO_2 assimilation rate under increased CO_2 concentration with sufficient nitrogen availability. Reduced photosynthesis has been reported at low soil N and ambient CO_2 concentrations (Domiciano et al. 2020). It has been reported that sufficient soil nitrogen combined with higher CO_2 concentrations induces carboxylation, resulting in an improved CO_2 assimilation rate (Bassi et al. 2018). It is well acknowledged that nitrogen is a limiting factor facilitating the photosynthesis process (Singh et al. 2010), and sufficient nitrogen can improve the Rubisco content and its activity together with chlorophyll content, resulting in enhanced carbon assimilation rate and plant productivity under elevated CO_2 conditions (Evans 1989; Shangguan et al. 2000; Yang et al. 2022).

The plants under aCO_2 and N_{200} had expressed lower transpiration rate (4.46 ± 0.19 mmol H_2O m^{-2} s^{-1}) by 39% than eCO_2 (6.21 ± 0.56 mmol H_2O m^{-2} s^{-1}) (Fig 3). Stomatal conductance was found to be maximum (0.44 ± 0.03 mol H_2O m^{-2} s^{-1}) under eCO_2 than aCO_2 (0.28 ± 0.02 mol H_2O m^{-2} s^{-1}) in N_{200} (Fig 3). Polley et al. (1999) reported a relationship between transpiration and soil N, noting that soil N availability and CO_2 concentration affect transpiration rate by altering plant nitrogen content. The present study showed that the combination of nitrogen application and increased CO_2 concentration significantly increased water loss through leaf transpiration (Fig. 3). The higher release of water molecules from the foliage could increase CO_2 gas exchange. Thus, due to the increased photosynthesis, more CO_2 is available to produce higher carbohydrates. These results were supported by gas exchange observations in cucumber plants exposed to similar conditions (Pinero et al. 2021). The increased gas exchange could be due to increased NH4+ in the leaves, which can acidify the cytoplasm and increase stomatal conductance (Hachiya and Sakakibara 2016). The acidification process can increase plasma membrane H+-ATPase activity, increasing leaf transpiration (Hedrich et al. 2001).

Water use efficiency (WUE) was increased by 16% under ambient CO_2 concentration (1.80 ± 0.23) compared to elevated CO_2 concentration (1.46 ± 0.10) in the high nitrogen application (N_{300}). However, nitrogen application has been reported to stimulate water use efficiency by *N. cadamba* when the CO_2 concentration in the environment increases

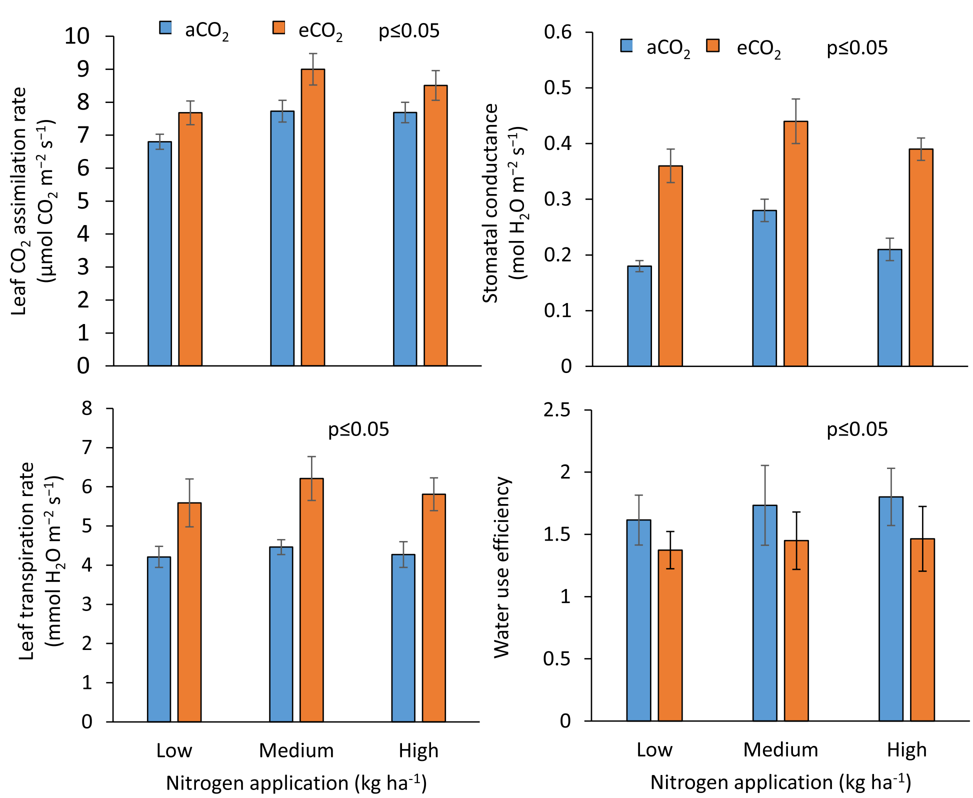

Fig. 3 Effect of nitrogen application (low-N_{200} Kg N ha^{-1}, medium-N_{300} Kg N ha^{-1}, and high-N_{500} Kg N ha^{-1}) on physiological traits of *N. cadamba* grown under CO_2 concentration (Ambient (aCO_2); 400 ± 14 µmol CO_2 mol^{-1}; Elevated (eCO_2); 800 ± 20 µmol CO_2 mol^{-1}). Error bars indicates the standard error of the mean. Results are mean of six replications (N=18)

(Fig. 3). Cruz et al. (2014) documented similar results with increased CO_2 concentration and N application. Torralbo et al. (2019) reported the opposite effect on the carbon assimilation rate in durum wheat, although similar responses were observed on water use efficiency.

It is widely recognized that different plant species exhibit diverse responses to increasing atmospheric CO_2 levels and the availability of soil nitrogen. These responses are reliant upon the unique and species-specific mechanisms governing photosynthesis and carbon exchange, as well as the plants' capacity to access and acquire nitrogen from the soil. In a changing climate, these plants may demonstrate contrasting nitrogen use efficiency and the allocation of nitrogen, along with other essential macro and micronutrients, among various plant parts, depending on soil nitrogen availability.

In certain situations, soil resources can lead to competition among different plant species for carbon and nitrogen resources. Consequently, plant species may respond differently to elevated CO_2 concentrations and nitrogen availability based on their specific photosynthetic pathways and nitrogen-fixing capabilities. This study investigated the impact of increasing atmospheric CO_2 levels and nitrogen applications, opening up a new opportunity to predict the responses of various plantation species under future climate changes and nitrogen limited conditions.

Therefore, the study recommends conducting long-term and systematic research to gain a comprehensive understanding of how plantation species respond to these factors and how their nitrogen requirements can be optimized to maximize the CO_2 fertilization effects. This is particularly pertinent in regions where current nitrogen management practices are inadequate. The data generated from such studies holds the potential to be instrumental in forecasting the likely effects of elevated CO_2 concentrations on plant species under varying nitrogen availability, as required by process-based dynamic global vegetation models. This knowledge is indispensable for advancing sustainable land management practices and enhancing scientific understanding of ecosystem dynamics in relation to climate change and nutrient availability.

Interlinking between biophysical, growth, and physiological functional traits

The interlinking between plant functional traits is depicted in Fig. 4. The analysis revealed significant correlations among biophysical, growth, and physiological plant traits. Among biophysical attributes, it was found that plant height exhibited strong correlations with the leaf CO_2 assimilation rate, stomatal conductance, water use efficiency, and transpiration rate (Fig. 4). Moreover, leaf area was identified as strongly correlated with leaf CO_2 assimilation rate, stomatal conductance, water use efficiency, and transpiration rate (Fig. 4).

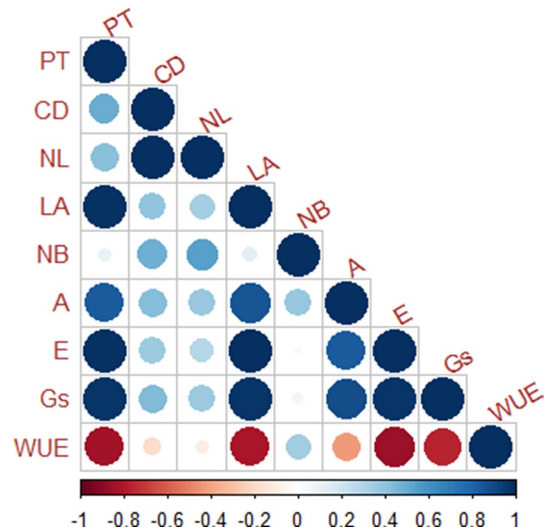

Fig. 4 Correlation between plant functional traits of *N. cadamba*. The symbols are denoted as follows: *PT*, plant height; *CD*, collar diameter; *NL*, numbers of leaves; *LA*, leaf area; *NB*, number of branches; *A*, leaf CO_2 assimilation rate; *E*, leaf transpiration rate; *Gs*, stomatal conductance; and *WUE*, water use efficiency

Understanding the interlinking between morphological, growth, and physiological parameters is essential in plant biology, from agriculture and forestry to ecological and conservation research. This understanding helps researchers and land managers make informed decisions about plant species and their resource requirements in diverse environments, which aid in developing strategies to adapt and mitigate climate change impacts and achieving sustainability targets.

Conclusion

This study has provided invaluable insights into the crucial role of soil nitrogen availability in shaping the effect of CO_2 fertilization on *N. cadamba*, an important urban plantation tree species. It is concluded that the magnitude of CO_2-induced growth enhancement and improved physiological responses is intricately linked to the nitrogen status of the soil. These findings stressed the significance of considering soil nutrient availability while planning urban tree planting initiatives to enhance urban green spaces (UGS) and mitigate the impacts of climate change. Moreover, the study suggested the imperative need for sustainable urban forestry practices, especially soil nutrient management, i.e., nitrogen supplementation, to optimize the benefits of elevated atmospheric CO_2 on tree growth and carbon sequestration in urban environments. The study may provide valuable guidance to urban planners and managers, enabling them to design and implement urban forestry strategies that foster healthier and more resilient urban ecosystems. Furthermore, this study contributes to global efforts to combat climate change by recognizing the complex interaction between soil nitrogen availability and CO_2 responsiveness in urban environments, aligning with the objectives of Sustainable Development Goals (SDGs).

Author contributions MS: Data curation, Writing- Original draft preparation, Visualization, Investigation. HS: Supervision, Conceptualization, Methodology, Writing- Reviewing and Editing. NK; MK; AK, SB and AT: Statistical analysis and Editing

Declarations

Conflict of interest The authors declared no conflict of interest while publishing this manuscript.

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