

## ORIGINAL RESEARCH



# Using leaf economic spectrum and photosynthetic acclimation to evaluate the potential performance of wintersweet under future climate conditions

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## Abstract

The function of landscape plants on the ecosystem can alleviate environmental issues of urbanization and global change. Global changes due to elevated CO<sub>2</sub> affect plant growth and survival, but there is a lack of quantitative methods to evaluate the adaptability of landscape plants to future climate conditions. Leaf traits characterized by leaf economic spectrum (LES) are the universal currency for predicting the impact on plant ecosystem functions. Elevated CO<sub>2</sub> usually leads to photosynthetic acclimation (PC), characterised by decreased photosynthetic capacity. Here, we proposed a theoretical and practical framework for the use of LES and PC to project the potential performance of landscape plants under future climatic conditions through principal component analysis, structural equation modelling, photosynthetic restriction analysis and nitrogen allocation analysis. We used wintersweet (an important landscaping species) to test the feasibility of this framework under elevated CO<sub>2</sub> and different nitrogen (N) supplies. We found that elevated CO<sub>2</sub> decreased the specific leaf area but increased leaf N concentration. The results suggest wintersweet may be characterized by an LES with high leaf construction costs, low photosynthetic return, and robust stress resistance. Elevated CO<sub>2</sub> reduced photosynthetic capacity and stomatal conductance but increased photosynthetic rate and leaf area. These positive physiological traits, e.g., larger leaf area (canopy), higher water use efficiency and stress resistance, may lead to improved performance of wintersweet under the predicted future climatic conditions. The results suggest planting more wintersweet in urban landscaping may be an effective adaptive strategy to climate change.

## 1 | INTRODUCTION

Continued urbanization and climate change are major challenges humans face in this century (IPCC, 2022; Dervishi et al., 2023). Urban vegetation is an important green infrastructure and is considered key to mitigating these adverse challenges (Velasco et al., 2016; Sousa-Silva et al., 2023). This is based on the biological traits of landscape plants, especially woody plants (Gratani and Varone, 2007a; Liu and Slik, 2022). Canopy shading and transpiration can alleviate the heat island effect caused by urbanization and improve people's thermal comfort (Dujardin

et al., 2022). Plants can reduce the magnitude of climate change by fixing atmospheric CO<sub>2</sub> in photosynthesis and improving air quality (Kim et al., 2020). The seasonal changes in leaf colour, flowers and fruits of plants enhance the natural experience and promote the aesthetic, as well as improve the mental health and increase the age of the residents (Stas et al., 2020; Dujardin et al., 2022; Tang et al., 2023). Landscape vegetation can also reduce the surface runoff of stormwater and noise pollution as well as improve microclimate conditions (Bae and Ryu, 2015; Stas et al., 2020; Downtin et al., 2023). and improve people's health and well-being (Dujardin et al., 2022; Tang et al., 2023).

Due to the unique and irreplaceable ecosystem service and functions, increasing the planting of landscape plants is encouraged in urban planning around the world (Nyelele and Kroll, 2021; Dervishi et al., 2023). It should be noted that poor health conditions of landscape plants can substantially reduce the magnitude of their services and functions (Simon et al., 2018; Esperon-Rodriguez et al., 2023). However, the options of plant species for landscaping are limited, and some species require higher maintenance and management costs than others (Lo Piccolo et al., 2023). Therefore, urban landscape planning requires a wealth of expertise (Ordóñez Barona et al., 2022). Only with a deep understanding of the environmental conditions of the planting site, the ecological requirements and physiological traits of different landscape tree species, and the needs of the community can the scientific species composition and the sustainability of green landscaping be achieved (Alizadeh and Hitchmough, 2020; Nyelele and Kroll, 2021). However, the eco-physiological performance of landscaping plant species in the future under the predicted new environmental conditions is generally poorly understood (Nitschke et al., 2017; Killi et al., 2018). Global change can affect the physiology, growth and survival of plants, but relevant research generally focuses on forest tree species and crops (Nitschke et al., 2017; Kim et al., 2020). The impact of climate change on the functions of urban landscape plants is rarely assessed (Falster et al., 2018; Esperon-Rodriguez et al., 2023). This lack of knowledge seriously restricts the development of proper adaptive strategies in urban landscape planning and predicting landscape plant performance under future climate conditions (Killi et al., 2018).

There is a coordinated relationship between leaf traits and plant functions, which can be used to predict plant responses to global changes (Cui et al., 2020). This is because leaf traits reflect the optimal phenotype the growing environment selects for the given range of resources and environmental conditions (Midolo et al., 2019). The leaf traits, including specific leaf area (SLA, ratio of unit leaf area to mass), leaf nitrogen concentration ( $N_{area}$ ), and net photosynthetic rate ( $A_n$ ) are known as leaf economic spectra (LES), which represent a broad trade-off between leaf structure and physiological and ecological traits (Onoda et al., 2017; Yang et al., 2019). SLA relates to leaf thickness and tissue density and affects the photosynthetic return on resource investment for leaf construction cost (Xiong and Flexas, 2018; Maenpuen et al., 2022). SLA is an important functional trait in LES and for plant growth analysis. Leaf traits are frequently measured in ecology to provide a ‘common currency’ for predicting how global change impacts plant ecosystem function and investment strategies for growth and survival (Firn et al., 2019; Lu et al., 2020).

Elevated atmospheric CO<sub>2</sub> is the foundation and driving force of the escalating global change (Wang et al., 2021). Due to intensive human activities and carbon emissions from the combustion of fossil fuels, CO<sub>2</sub> concentrations in urban areas are significantly higher than in natural environments (Gratani and Varone, 2007b). Recent studies have found that while all landscape plant species fix CO<sub>2</sub> via photosynthesis, the photosynthetic capacity (PC: maximum carboxylation rate ( $V_{cmax}$ ) and maximum electron transfer rate ( $J_{max}$ )) varies as much as 2–8 times between different tree species used in landscaping

(Kimm and Ryu, 2015; Lo Piccolo et al., 2023). However, the effects of elevated CO<sub>2</sub> on the physiology and growth of landscape plants are rarely reported. The limited literature suggests that elevated CO<sub>2</sub> can change the growth rate of ornamental plants (Kim et al., 2020). The plants growing under emulated future CO<sub>2</sub> usually exhibit typical photosynthetic acclimation, such as decreased PC and stomatal conductance ( $g_s$ ) (Knauer et al., 2019; Pao et al., 2019; Smith and Keenan, 2020). As a substrate of photosynthesis, elevated CO<sub>2</sub> generally increases carbohydrate and biomass production. Without a corresponding increase in nitrogen supply and uptake, such an increase will lead to a decrease in nitrogen concentration in the plant, particularly in the leaf, triggering a decline in photosynthetic capacity, i.e., photosynthetic acclimation (Silva-Pérez et al., 2020; Ainsworth and Long, 2021; Krämer et al., 2022). Thus, proper assessment of photosynthetic acclimation to elevated CO<sub>2</sub> may be key for predicting plant response to global change.

Wintersweet (*Chimonanthus praecox* L.) is widely used in landscaping in temperate regions (Shang et al., 2020). It blooms in winter with a sweet fragrance and has high ornamental value. Wintersweet has a unique and irreplaceable position in urban parks due to its unique timing of flowering and fresh, sweet smell (Tian et al., 2019a; Song and Wu, 2022). It is often used by landscape architects as an ornamental highlight for landscape routes and an esthetic attraction to visitors in the winter (Shen et al., 2021). Past studies of wintersweet mainly focus on its floral fragrance and drought resistance (Anirban, 2019; Tian et al., 2019b), and its acclimation to future climate conditions, such as elevated CO<sub>2</sub>, has not been reported. Enrichment of CO<sub>2</sub> typically promotes plant biomass, which dilutes the leaf nitrogen concentration in leaves and, in turn, affects photosynthetic capacity and nitrogen supply, influencing the leaf traits in the LES (Ainsworth and Long, 2021). This study investigated the responses of the LES and photosynthetic traits to elevated CO<sub>2</sub> and variations in nitrogen supply under controlled environmental conditions. The results of this study provide a theoretical and practical framework for quantifying and predicting the physiological and growth performance of landscape plants under the predicted future climate conditions and for landscape planning. Our methodologies should also be useful for evaluating the potential performance of other landscape woody species under the predicted future climate conditions.

## 2 | MATERIALS AND METHODS

### 2.1 | Plant materials and treatments

The seeds of wintersweet were collected from the landscape arboretum at the Zhejiang A&F University campus (30.2374 N, 119.7284E). The seeds were stratified in wet sand at 4°C for about 60 days before being sown in germination trays. Seedlings were transplanted into 4 L plastic pots filled with vermiculite and peat moss (1:1, v:v) (Sun Gro®).

The experiment was conducted in four phytotrons on the Thunder Bay campus of Lakehead University. The experiment followed a split-plot design with two [CO<sub>2</sub>] levels (ambient 400 μmol mol<sup>-1</sup>

(aCO<sub>2</sub>) and elevated 800 μmol mol<sup>-1</sup> (eCO<sub>2</sub>) as the main plot, and three nitrogen levels as the split-plot (containing 3 mM (N3), 6 mM (N6), and 9 mM (N9) nitrogen). Each CO<sub>2</sub> level had two replicates (two separate phytotrons). Each replicate of each treatment combination had 8 seedlings (a total of 96 seedlings: 2 CO<sub>2</sub> \* 2 replicates \* 3 N forms \* 8 seedlings).

The nitrogen treatments used ammonium nitrate (BioBasic Inc.). All N treatments received identical concentrations of other nutrient elements: 5 mM Potassium phosphate and 4 g L<sup>-1</sup> Micromax Micronutrients Granular (calcium 6%, magnesium 3%, sulphur 12%, boron 0.1%, copper 1%, iron 17%, manganese 2.5%, molybdenum 0.05%, zinc 1%) (Everris NA Inc.). The seedlings were fertilized twice weekly and irrigated with 500 mL water every other day. The positions of the seedlings were randomly changed within the same phytotron and between the replicate phytotrons of each CO<sub>2</sub> treatment every two weeks.

The CO<sub>2</sub> concentration in each phytotron was maintained using a CO<sub>2</sub> generator (GEN-2E, Custom Automated Products Inc.). Other environmental conditions in all the phytotrons were 25/16°C (day/night) temperature, 50% RH and 16-h photoperiod. High-pressure sodium lamps (P.L. Systems) were used to supplement the natural light when the ambient light intensity was below 500 μmol m<sup>-2</sup> s<sup>-1</sup> or the natural day length was shorter than 16-h. All the environmental variables in each phytotron were monitored and controlled by an Argus Titan Environment system (Argus Control Systems Ltd.).

## 2.2 | Gas exchange and pigment measurement

Three seedlings were randomly selected from each treatment combination, and foliar gas exchange was measured between 9:00 and 16:00 on an unshaded mature leaf near the top of the canopy using a LI-6800 Portable Photosynthesis System (LI-COR Biosciences). The gas exchange under treatment CO<sub>2</sub> was measured at the corresponding treatment [CO<sub>2</sub>] (aCO<sub>2</sub> at 400 μmol mol<sup>-1</sup>, eCO<sub>2</sub> at 800 μmol mol<sup>-1</sup>), 25°C temperature, 1.1–1.3 kPa water vapour pressure deficit, 1000 μmol m<sup>-2</sup> s<sup>-1</sup> photosynthetically active radiation flux density. At least 30 min was allowed before a steady state reading was taken. The net photosynthetic rate ( $A_{n-g}$ ), stomatal conductance ( $g_s$ ), intercellular [CO<sub>2</sub>] to ambient [CO<sub>2</sub>] ratio ( $C_i/C_a$ ), and photosynthetic nitrogen uses efficiency ( $PNUE = A_{n-g}/N_{area}$ ) were subjected to statistical analyses. Instantaneous photosynthetic water use efficiency ( $iWUE = A_{n-g}/E$ , where  $E$  is the corresponding transpiration rate).

Photosynthetic response to intercellular [CO<sub>2</sub>] ( $A/C_i$ ) curves were measured at 400, 300, 200, 100, 50, 400, 500, 600, 800, 1000, 1200, 1500 μmol mol<sup>-1</sup> [CO<sub>2</sub>] at the same temperature, VPD, and PAR as given previously. The maximum rate of Rubisco carboxylation  $V_{max}$  and maximum rate of photosynthetic electron transport  $J_{max}$  were estimated using the fitaci function, and the transition point ( $C_{i-t}$ ,  $A_{n-t}$ ) of biochemical limitation from Rubisco to RuBP regeneration was estimated using findCiTranstion function in the Plantecophys R package from  $A/C_i$  data (Duursma, 2015). The initial slope of the  $A/C_i$  curve was used as the apparent carboxylation efficiency (ACE).

The initial portion of three  $A/C_i$  curves was measured under 200, 150, 100, and 50 μmol mol<sup>-1</sup> of [CO<sub>2</sub>], and 300, 150, and 75 μmol m<sup>-2</sup> s<sup>-1</sup> PAR, and used to estimate the daytime respiratory rate ( $R_d$ ) and intercellular CO<sub>2</sub> compensation point ( $C_i^*$ ) using the Walker's slope intercept method (Walker et al., 2016). The variable  $J$  method was employed to calculate mesophyll conductance ( $g_m$ ) (Harley et al., 1992), using the equation  $\Gamma^* = C_i^* + R_d / g_m$  (Walker et al., 2016), where  $\Gamma^*$  is the CO<sub>2</sub> compensation point in the absence of day respiration.

After the gas exchange measurement, the sample leaves were immediately removed and stored in a refrigerator (-35°C). Leaf pigment was extracted using 80% acetone, and the 645 and 663 nm absorbance was measured. The leaf chlorophyll concentration ( $Chl$ ) was calculated with  $Chl = 20.2 * A_{645} + 8.02 * A_{663}$ , where  $A_{645}$  and  $A_{663}$  are the absorbance at 645 nm and 663 nm, respectively (Wellburn, 1994).

## 2.3 | Relative photosynthetic limitation and nitrogen partitioning

The relative limitations of photosynthesis by biochemical ( $l_b$ ), mesophyll conductance ( $l_m$ ) and stomatal conductance ( $l_s$ ) limitations were calculated according to Elferjani (Elferjani et al., 2021):  $l_b = g_t / (g_t + \partial A_n / \partial C_c)$ ;  $l_s = (g_t / g_s * \partial A_n / \partial C_c) / (g_t + \partial A_n / \partial C_c)$ ;  $l_m = (g_t / g_m * \partial A_n / \partial C_c) / (g_t + \partial A_n / \partial C_c)$ , where  $g_t$  is the total conductivity to CO<sub>2</sub> diffusion ( $g_t = 1 / (1 / g_m + 1 / g_s)$ ),  $\partial A_n / \partial C_c$  is the initial slope of the  $A_n$  to  $C_c$  response curve and was calculated using the equation  $\partial A_n / \partial C_c = V_{cmax} / (\Gamma^* + K_m)$  (Farquhar et al., 1980), where  $\Gamma^*$  was as noted previously and  $K_m$  was calculated by  $K_m = K_c (1 + O / K_o)$  (Bernacchi et al., 2001). Stomatal limitation ( $l_s$ ) was calculated using  $(C_a - C_i)/C_a$ ,  $C_a$  and  $C_i$  are CO<sub>2</sub> concentrations around the leaf and intercellular space, respectively. The partitioning of leaf nitrogen (N) into carboxylation ( $N_c$ ), electron transfer ( $N_e$ ) and light capture ( $N_v$ ) was calculated using the Trouwborst method (Trouwborst et al., 2011).

## 2.4 | Biomass and nitrogen measurement

After all the above measurements, the height of all the seedlings was measured. Leaf area was measured using a Regent WinFolia system (Regent Instruments Inc.). The seedlings were then harvested and separated into roots, stems, and leaves, and oven-dried at 75°C for 48 h to constant weight to determine the biomass of different organs and SLA. Area-based leaf N concentration ( $N_{area}$ ) and carbon concentration (C) were measured using the dry combustion method on a CNS-2000 (LECO Corp.) at the Lakehead University Centre for Analytical Services.

## 2.5 | Statistical analysis

The effects of CO<sub>2</sub> and N levels on photosynthetic and growth traits of individual seedlings were investigated using a two-way analysis of

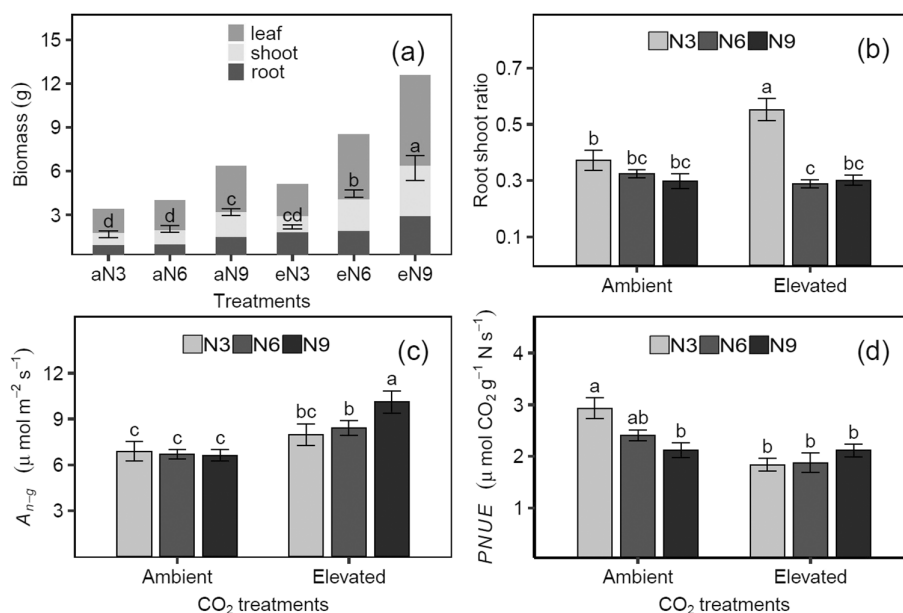
variance using the agricolae package in R 4.2.4. A three-way ANOVA was performed on  $A_{n-g}$  and  $PNUE$ . Logarithmic or power transformation was used to transform variables that did not meet the normality and homogeneity assumptions before the ANOVA. When an interaction or N effect was statistically significant, LSD post hoc pairwise comparisons were conducted for the means. The PCA function of the FactoMineR package was used for principal component analysis (PCA) to investigate the relationship and clustering of physiological and growth-related parameters. The Bowen method (Bowen et al., 2017) was used to investigate the direct/indirect effects of  $CO_2$  and N levels as categorical variables on biomass and  $A_{n-g}$  using the structural equation model (SEM) and the psem function in the piecewiseSEM package (Lefcheck, 2016). Based on the LES and a prior structural model (Onoda et al., 2017; Liu et al., 2022), biomass was explained by

$A_{n-g}$ ,  $N_{area}$  and  $SLA$  (Figure 8a), and  $A_{n-g}$  was explained by photosynthetic capacity,  $Chl$  and  $g_t$  (Figure 8b). The photosynthetic capacity was obtained by the regression equations from  $V_{cmax}$  and  $J_{max}$ .

### 3 | RESULTS

#### 3.1 | Biomass and leaf area increased under elevated $CO_2$ and N enrichment

Elevated  $CO_2$  and increased N supply promoted biomass and total leaf area production in wintersweet, and the values in the eN9 treatment combination were substantially higher than in any other treatments (Figure 1, Table 1). In contrast, e $CO_2$  significantly reduced  $SLA$ ; the



**FIGURE 1** Effects of  $CO_2$  and N levels on biomass (a), root shoot ratio (b), photosynthetic rate at growth  $CO_2$  ( $A_{n-g}$ , c) and photosynthetic nitrogen use efficiency ( $PNUE$ , d) in wintersweet. “a-” means ambient  $CO_2$  ( $400 \mu mol mol^{-1}$ ) and “e-” means elevated  $CO_2$  ( $800 \mu mol mol^{-1}$ ) treatments. N3, N6 and N9 mean that fertilized 3 mM, 6 mM and 9 mM nitrogen respectively. Means ( $\pm$  SE,  $n = 6$ ) with different letters indicated significant differences between treatments (Tukey host hoc test,  $P < 0.05$ ).

**TABLE 1** Leaf morphological and photosynthetic traits, and nitrogen concentration of wintersweet grown at ambient and elevated  $CO_2$  response different N levels.

$CO_2$	N	Leaf area ( $cm^{-2}$ )	$SLA$ ( $cm^2 g^{-1}$ )	$N_{area}$ ( $g m^{-2}$ )	C/N	$L_s$	$iWUE$
a $CO_2$	N3	483 $\pm$ 31 c	143.6 $\pm$ 7.6 a	2.1 $\pm$ 0.1 c	14.1 $\pm$ 0.6 b	0.46 $\pm$ 0.02 bc	7.4 $\pm$ 0.3 ab
	N6	570 $\pm$ 26 c	143.3 $\pm$ 3.9 a	2.3 $\pm$ 0.1 bc	13.4 $\pm$ 0.3 bc	0.58 $\pm$ 0.04 a	7.4 $\pm$ 0.4 ab
	N9	861 $\pm$ 37 b	135.5 $\pm$ 5.2 a	2.6 $\pm$ 0.1 b	12.3 $\pm$ 0.2 c	0.53 $\pm$ 0.04 ab	7.9 $\pm$ 0.6 a
e $CO_2$	N3	463 $\pm$ 31 c	90.7 $\pm$ 4.4 c	2.3 $\pm$ 0.1 bc	20.1 $\pm$ 0.6 a	0.43 $\pm$ 0.04 cd	6.7 $\pm$ 0.4 ab
	N6	1024 $\pm$ 54 b	120.1 $\pm$ 3.8 b	2.7 $\pm$ 0.1 b	13.9 $\pm$ 0.4 b	0.35 $\pm$ 0.04 d	6.5 $\pm$ 0.4 b
	N9	1325 $\pm$ 91 a	105.8 $\pm$ 4.1 b	3.2 $\pm$ 0.1 a	13 $\pm$ 0.1 bc	0.41 $\pm$ 0.03 cd	6.7 $\pm$ 0.6 ab
P-value	$CO_2$	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	<b>0.021</b>
	N	< 0.001	0.018	< 0.001	< 0.001	0.7	0.73
	$CO_2$ -N	< 0.001	<b>0.015</b>	0.24	< 0.001	<b>0.03</b>	0.83

Note: each value represents mean  $\pm$  SE ( $n = 6$ ). Two-way ANOVA was performed on the effects of  $CO_2$ , nitrogen (N), and their interaction. Significant effects ( $P \leq 0.05$ ) are shown in bold. Different letters within the same column indicated statistically significant differences between treatments (Tukey post hoc test,  $P < 0.05$ ). a $CO_2$ : ambient  $CO_2$  ( $400 \mu mol mol^{-1}$ ); e $CO_2$ : elevated  $CO_2$  ( $800 \mu mol mol^{-1}$ ); N3, N6 and N9 mean that fertilized 3 mM, 6 mM and 9 mM nitrogen respectively.  $SLA$ : specific leaf area;  $N_{area}$ : leaf N content based on leaf-area; C/N: leaf carbon-nitrogen ratio;  $L_s$ : stomatal limitation;  $iWUE$ : intrinsic water use efficiency.

effect was the largest at N3 (Table 1). Furthermore, wintersweet tended to allocate more biomass to the root system under N3 than the other two N treatments (Figure 1b).

### 3.2 | Leaf N centration, N use efficiency and N distribution

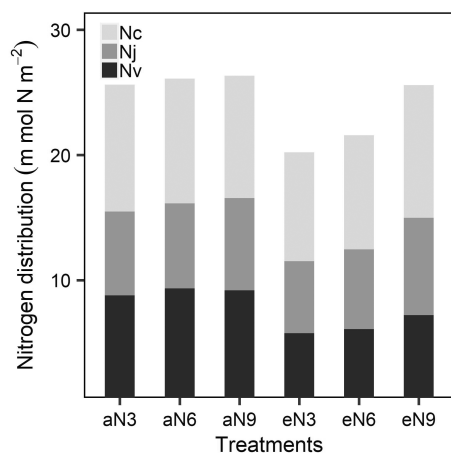
$N_{area}$  increased with the increase in nitrogen supply and  $CO_2$  elevation (Table 1). Elevated  $CO_2$  generally increased, but increasing N supply decreased, the leaf C/N ratio, although not all the effects were statistically significant (Table 1).

Increases in N supply significantly decreased PNUE under a $CO_2$  but had no significant effect under e $CO_2$  (Figure 1d). The e $CO_2$  reduced N allocation to the photochemical apparatus of photosynthesis (Figure 2). The effect of decreasing N supply on N allocation to the biochemical machinery of photosynthesis, however, varied with  $CO_2$  treatment, ranging from having no effects under a $CO_2$  and decreasing it under e $CO_2$  (Figure 2).

### 3.3 | Photosynthetic traits and limitations to photosynthesis

e $CO_2$  significantly increased  $A_{n-g}$  in all the N treatments, but the highest N treatment (N9) significantly increased  $A_{n-g}$  only under e $CO_2$  (Figure 1b). The photosynthesis of wintersweet was limited the most by stomatal resistance (more than 50%) and least by mesophyll resistance (Figure 3). Treatment effects on the traits of A/Ci curves were demonstrated in Figure 4.

Neither  $CO_2$  nor N supply significantly affected leaf chlorophyll concentration (Table 2). The e $CO_2$  treatment generally reduced  $g_m$



**FIGURE 2** Leaf N partitioning into carboxylation ( $N_c$ ), electron transfer ( $N_j$ ), and light capture systems ( $N_v$ ) in response to  $CO_2$  and different N levels in wintersweet. “a-” means ambient  $CO_2$  ( $400 \mu\text{mol mol}^{-1}$ ) and “e-” means elevated  $CO_2$  ( $800 \mu\text{mol mol}^{-1}$ ) treatments. N3, N6 and N9 mean that fertilized 3 mM, 6 mM and 9 mM nitrogen respectively.

and  $g_s$ , but the effects were not statistically significant in all the N treatments (Table 2). e $CO_2$ , however, significantly increased  $C_i/C_a$  in all the N treatments (Table 2).

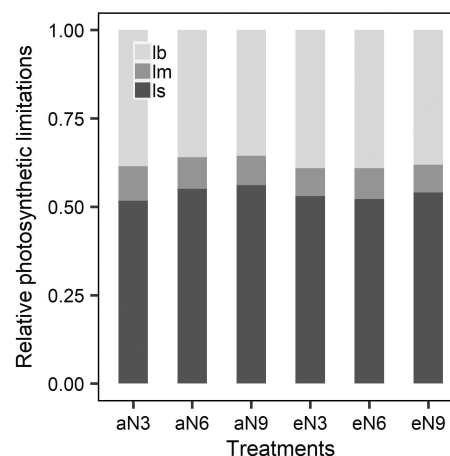
### 3.4 | Acclimation to $CO_2$ and N supply

PCA results showed that seedlings grown under a $CO_2$  converged on the ellipse in the directions of  $L_s$ ,  $SLA$ ,  $iWUE$  and  $PNUE$  (on the left of Figure 5a), while seedlings grown under e $CO_2$  converged on the  $A_{n-t}$ ,  $N_{area}$ , biomass,  $A_{n-g}$ , C/N and  $C_{i-t}$  ellipse (on the right of Figure 5a).  $L_s$  and  $SLA$  on the left were inversely proportional to  $C_{i-t}$ ,  $C_i/C_a$ , and  $C_{i-g}$  on the right (Figure 5). With increases in N supply, corresponding ellipses rotated counterclockwise upward (Figure 5b). The seedlings grown under low N supply tended to maintain C/N, while those in high nitrogen treatments were characterized by high values in  $J_{max}$ ,  $A_{max}$ ,  $A_{n-t}$ ,  $N_{area}$ , biomass, and  $A_{n-g}$  (Figure 5b).

## 4 | DISCUSSION

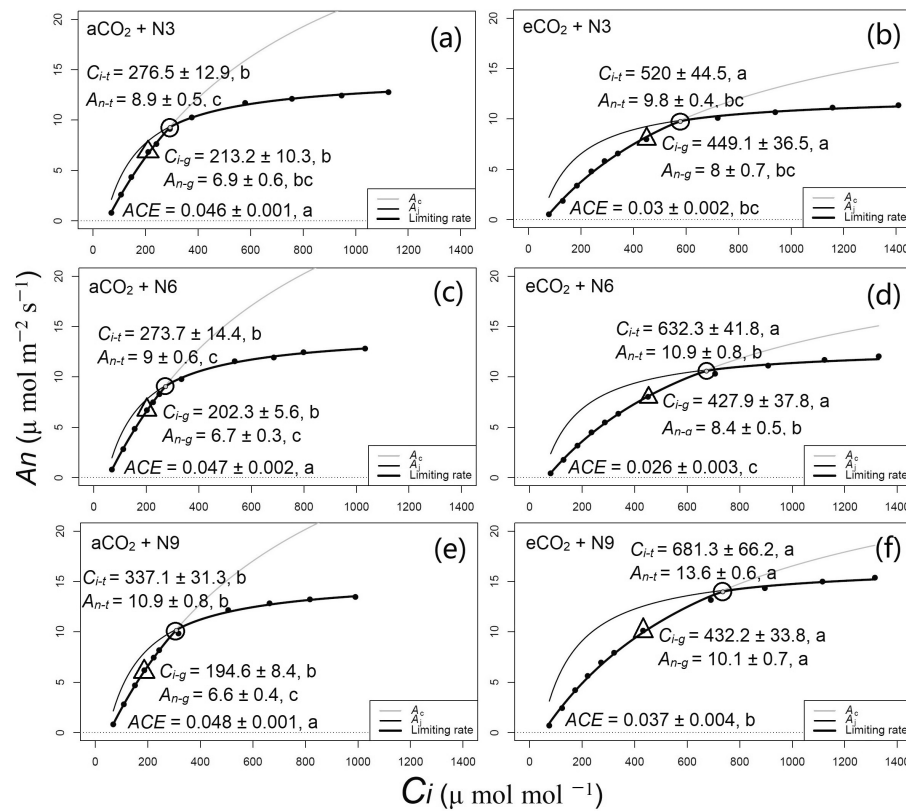
### 4.1 | Leaf economic spectrum and leaf traits

The LES mainly involves  $SLA$ ,  $N_{area}$ , PC, and  $A_n$ , and the core parameters are  $SLA$  and  $N_{area}$  (Onoda et al., 2017; Yang et al., 2019). PC and  $A_n$  are also key to photosynthetic acclimation (Smith and Keenan, 2020; Tcherkez et al., 2020), and  $A_n$  is affected by photosynthetic limitations.  $SLA$  or leaf mass per unit leaf area ( $1/SLA$ ) is related to leaf thickness and leaf mass density (Maenpuen et al., 2022), reflecting the construction cost of PC (Onoda et al., 2017).  $N_{area}$  reflects the nitrogen used for photosynthesis and growth (structure and metabolism) (Krämer et al., 2022). As nitrogen related to photosynthesis usually accounts for about 50% of the total nitrogen content in leaves, there



**FIGURE 3** The relative limitations of photosynthesis by biochemistry ( $l_b$ ), and mesophyll resistance ( $l_m$ ), and stomatal resistance ( $l_s$ ) in response to  $CO_2$  and N supply in wintersweet. N3, N6 and N9 mean that fertilized 3 mM, 6 mM and 9 mM nitrogen respectively. Abbreviations are provided in Table S1.





**FIGURE 4** The  $A/C_i$  curves in response to different N levels wintersweet seedlings grown under ambient  $\text{CO}_2$  ( $\text{aCO}_2$ ) and elevated  $\text{CO}_2$  ( $\text{eCO}_2$ ). N3, N6 and N9 mean that fertilized 3 mM, 6 mM and 9 mM nitrogen respectively. Each point denotes the means of six ( $C_i$ ,  $A_n$ ) values in  $A/C_i$  curve. The circles represent the transition point ( $C_{i-t}$ ,  $A_{n-t}$ ) from Rubisco carboxylation to RuBP regeneration of photosynthesis limitation. The triangles indicated the photosynthetic rate ( $C_{i-g}$ ,  $A_{n-g}$ ) under growth  $C_a$  ( $400 \mu\text{mol mol}^{-1}$  versus  $800 \mu\text{mol mol}^{-1}$ ). ACE: apparent carboxylation efficiency estimated from the initial slope of  $A/C_i$  curve. Different letters of the same parameter in the same species are significantly different between treatments (Tukey host hoc test,  $P < 0.05$ , see Table S2).

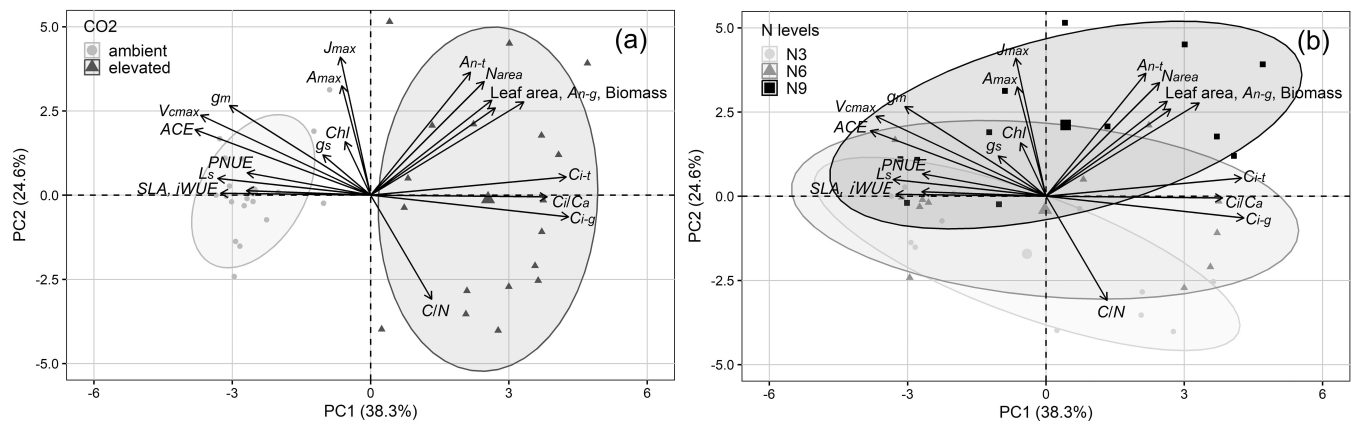
**TABLE 2** Photosynthetic capacity, chlorophyll concentration, conductance to  $\text{CO}_2$  diffusion, and intercellular to external  $\text{CO}_2$  concentration ratio in wintersweet grown at ambient or elevated  $\text{CO}_2$  in response to different N levels.

$\text{CO}_2$	N	$V_{\text{cmax}}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	$J_{\text{max}}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	Chl ( $\text{mg m}^{-2}$ )	$g_m$ ( $\text{mol m}^{-2} \text{s}^{-1}$ )	$g_s$ ( $\text{mmol m}^{-2} \text{s}^{-1}$ )	$C_i/C_a$
a $\text{CO}_2$	N3	$39.5 \pm 1$ a	$63.4 \pm 2$ ab	$350.4 \pm 16.5$ a	$0.21 \pm 0.011$ ab	$42 \pm 5.9$ a	$0.43 \pm 0.02$ b
	N6	$41.9 \pm 1.5$ a	$64.3 \pm 2.9$ ab	$344.4 \pm 11.2$ a	$0.22 \pm 0.003$ a	$37.1 \pm 2.3$ ab	$0.41 \pm 0.01$ b
	N9	$41.2 \pm 1$ a	$69.8 \pm 3.3$ ab	$338.1 \pm 10.4$ a	$0.24 \pm 0.009$ a	$36 \pm 3.9$ ab	$0.42 \pm 0.03$ b
e $\text{CO}_2$	N3	$25.8 \pm 2.8$ c	$54.7 \pm 3.4$ b	$300.2 \pm 29.9$ a	$0.17 \pm 0.012$ bc	$26.2 \pm 3.9$ b	$0.53 \pm 0.04$ a
	N6	$27.3 \pm 2.6$ bc	$60.5 \pm 5.2$ ab	$315.2 \pm 27.7$ a	$0.16 \pm 0.011$ c	$29.2 \pm 6$ ab	$0.6 \pm 0.05$ a
	N9	$32.3 \pm 3.1$ b	$73.7 \pm 4.6$ a	$366.7 \pm 31.2$ a	$0.21 \pm 0.017$ ab	$31.2 \pm 3.7$ ab	$0.56 \pm 0.03$ a
P-value	$\text{CO}_2$	<b>&lt; 0.001</b>	0.34	0.37	<b>&lt; 0.001</b>	<b>0.01</b>	<b>&lt; 0.001</b>
	N	0.18	<b>&lt; 0.001</b>	0.46	<b>0.01</b>	0.98	0.82
	$\text{CO}_2 \times \text{N}$	0.38	0.25	0.22	0.28	0.46	0.49

Note: each value represents mean  $\pm$  SE ( $n = 6$ ). Two-way ANOVA was performed on the effects of  $\text{CO}_2$ , nitrogen form (N), and their interactions ( $\text{CO}_2 \times \text{N}$ ). Significant effects ( $P \leq 0.05$ ) are marked in bold and “\*” indicates interaction. Different letters within the same column indicated statistically significant differences between treatments (Tukey post hoc test,  $P < 0.05$ ). a $\text{CO}_2$ : ambient  $\text{CO}_2$  ( $400 \mu\text{mol mol}^{-1}$ ); e $\text{CO}_2$ : elevated  $\text{CO}_2$  ( $800 \mu\text{mol mol}^{-1}$ ); N3, N6 and N9 mean that fertilized 3 mM, 6 mM and 9 mM nitrogen respectively.  $V_{\text{cmax}}$ : maximum rate of ribulose-1,5-bisphosphate carboxylation;  $J_{\text{max}}$ : maximum photosynthetic electron transport rate; Chl: leaf chlorophyll concentration.  $g_m$ : mesophyll conductance;  $g_s$ : stomatal conductance;  $C_i/C_a$ : intercellular ( $C_i$ ) to ambient ( $C_a$ )  $\text{CO}_2$  concentration ratio.

is a trade-off in nitrogen allocation between photosynthesis and growth (Silva-Pérez et al., 2020). Therefore, investigating changes in SLA and  $N_{\text{area}}$  under different environments is a classic methodology for analyzing plant functions by LES (Onoda et al., 2017; Xiong and Flexas, 2018). At one end of the LES are higher SLA and  $N_{\text{area}}$ , indicating that a given investment in leaf biomass will lead to a larger light-intercepting area and, higher returns in carbohydrates produced and faster growth. These traits are associated with invasive plant species

(Onoda et al., 2017; Cui et al., 2020). The other end of the LES is associated with higher leaf structure investments, lower returns in carbohydrate production and, slower growth but longer leaf lifespan and robust stress tolerance (Xiong and Flexas, 2018). However, the existence of these relationships depends on sufficient resources (Onoda et al., 2017). Our results showed no synchronous change in SLA and  $N_{\text{area}}$ , and elevated  $\text{CO}_2$  significantly reduced SLA but increased  $N_{\text{area}}$ ,



**FIGURE 5** Principal Component Analysis (PCA) on growth and photosynthetic parameters in wintersweet exposed to CO<sub>2</sub> (a) and N levels (b) treatments. The arrows point to near overlap, vertical, and reverse, which represent positive, no, and negative correlations between these parameters respectively. N3, N6 and N9 mean that fertilized 3 mM, 6 mM and 9 mM nitrogen respectively.  $A_{n-t}$ : net photosynthesis rate at transition point ( $C_{i-t}$ ,  $A_{n-t}$ ) between Rubisco limitation and RuBP regeneration limitation based on  $A/C_i$  curve;  $N_{area}$ : leaf N per unit area;  $C_i/C_a$ : the ratio of  $C_i$  and  $C_a$ ;  $A_{n-g}$ : net photosynthesis rate at a growth [CO<sub>2</sub>] which eCO<sub>2</sub> at 800  $\mu\text{mol mol}^{-1}$  and aCO<sub>2</sub> at 400  $\mu\text{mol mol}^{-1}$ ; C/N: leaf carbon and nitrogen ratio;  $A_{max}$ : photosynthetic rate of saturation light at 400  $\mu\text{mol mol}^{-1}$ ;  $L_s$ : stomatal limitation;  $iWUE$ : intrinsic water use efficiency;  $SLA$ : specific leaf area;  $PNUe$ : photosynthesis nitrogen use efficiency;  $ACE$ : apparent carboxylation efficiency estimated from the initial slope of  $A/C_i$  curve;  $V_{cmax}$ : maximum rate of ribulose-1,5-bisphosphate carboxylation;  $g_m$ : mesophyll conductance;  $g_s$ : stomatal conductance;  $Chl$ : leaf chlorophyll concentration;  $J_{max}$ : maximum of photosynthetic electron transport rate. See Table S1 for other explanations.

suggesting that elevated CO<sub>2</sub> might promote wintersweet's growth, lifespan, and stress resistance.

Elevated CO<sub>2</sub> generally improves carbon fixation and biomass production, diluting leaf nitrogen concentration and reducing photosynthetic capacity (Ainsworth and Long, 2021). However, our results show that eCO<sub>2</sub> reduced PC and chlorophyll concentration but increased  $N_{area}$ , indicating a reduction of N allocation to photosynthetic apparatus, particularly light-harvesting pigments ( $N_v$ ). It is unclear where the nitrogen saved from the reduction of the allocation to photosynthetic apparatus was allocated. However, this change in N allocation did reduce the photosynthetic nitrogen use efficiency in seedlings grown under eCO<sub>2</sub>, although eCO<sub>2</sub> significantly increased  $A_{n-g}$ .  $PNUe$  is closely related to the proportion of leaf N allocated to photosynthesis (mainly to Rubisco) (Onoda et al., 2017). Our principal component analysis and deconstructed equation model results suggest that increasing nitrogen supply appears to have compensated for the negative effects of elevated CO<sub>2</sub> on photosynthetic capacity. Therefore, the elevated CO<sub>2</sub> and higher nitrogen supply synergistically affected the growth of Wintersweet.

## 4.2 | Acclimation to elevated CO<sub>2</sub> and biochemical limitations to photosynthesis

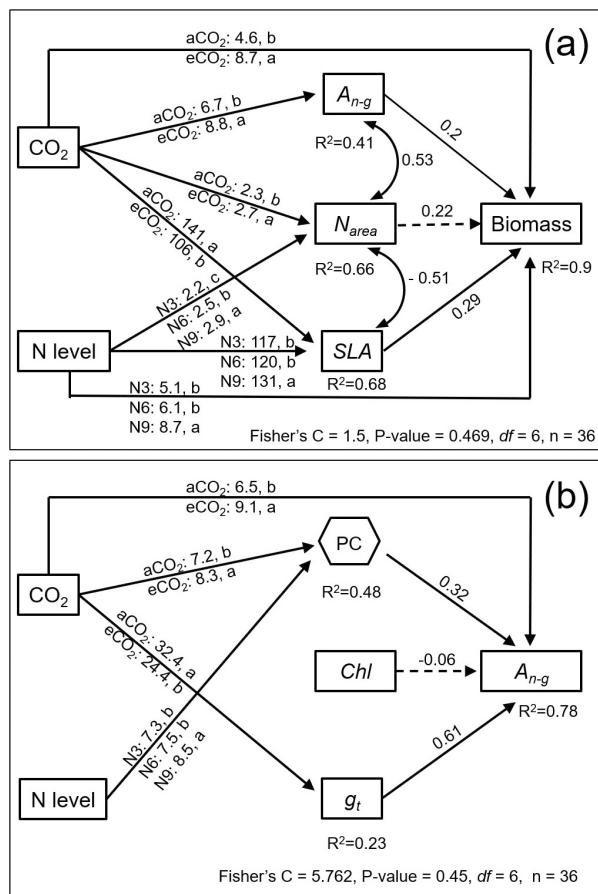
Elevated CO<sub>2</sub> usually decreases  $V_{cmax}$  and  $J_{max}$ , a phenomenon known as photosynthetic acclimation or downregulation (Smith and Keenan, 2020; Tcherkez et al., 2020). CO<sub>2</sub> is a substrate for photosynthesis, and a higher concentration will reduce the substrate limitation for photosynthesis, leading to a decrease in N allocation to photosynthetic machinery (Silva-Pérez et al., 2020). We observed that

Wintersweet exhibited a typical photosynthetic acclimation reaction. The effect of photosynthetic downregulation, however, is generally smaller than the stimulation of photosynthesis by the elevation of CO<sub>2</sub>, resulting in a higher actual rate of  $A_{n-g}$  under eCO<sub>2</sub> than under aCO<sub>2</sub> (Wang et al., 2022), as we have observed in this current study.

The eCO<sub>2</sub> did not change the primary limitation of photosynthesis in wintersweet. Some previous studies have reported that the elevation of CO<sub>2</sub> can trigger the shift of the primary limitation of photosynthesis from biochemical limitation (i.e.,  $V_{cmax}$  limitation,  $A_{n-g} < A_{n-t}$ ) to photochemical limitation (i.e., limitation by  $J_{max}$ ,  $A_{n-g} > A_{n-t}$ ) (Wang et al., 2023). However, the photosynthesis of wintersweet was still primarily limited by  $V_{cmax}$  under eCO<sub>2</sub> in this study (Figure 4). Furthermore, the eCO<sub>2</sub> significantly reduced leaf chlorophyll concentration in wintersweet, which is generally positively correlated to light harvesting and photosynthetic electron transport. These results suggest that the resistance to CO<sub>2</sub> diffusion from the atmosphere to the carboxylation site in the chloroplast will likely continue to exert a major limitation to the photosynthesis of wintersweet in the future with elevated CO<sub>2</sub>.

## 4.3 | CO<sub>2</sub> diffusion limitations to photosynthesis

An interesting finding of this study is that wintersweet had very low stomatal conductance, less than 50  $\text{mmol m}^{-2} \text{s}^{-1}$  in all treatments, which is much lower than typical values for deciduous broad-leaved tree species under non-stress conditions (Wang et al., 2022). In contrast, the mesophyll conductance values,  $g_m$ , were comparable to those reported for other deciduous tree species (Elferjani et al., 2021). For most tree species, the values of  $g_s$  and  $g_m$  are about equal (Wang and Dang, 2022). The  $g_s$  of wintersweet, however, was only about 1/6



**FIGURE 6** The *priori* (showing all tested paths) piecewise structural equation model (pSEM) relating to direct and indirect effects of CO<sub>2</sub> and N levels on biomass and  $A_{n-g}$ . Two CO<sub>2</sub> treatments (ambient CO<sub>2</sub>: 400  $\mu\text{mol mol}^{-1}$  and elevated CO<sub>2</sub>: 800  $\mu\text{mol mol}^{-1}$ ) and N levels (fertilized 3 mM (N3), 6 mM (N6) and 9 mM (N9) nitrogen) are treated as categorical variables.  $A_{n-g}$ : net photosynthesis rate at a growth [CO<sub>2</sub>] which eCO<sub>2</sub> at 800  $\mu\text{mol mol}^{-1}$  and aCO<sub>2</sub> at 400  $\mu\text{mol mol}^{-1}$ ;  $N_{area}$ : leaf N per unit area; SLA: specific leaf area; *Chl*: leaf chlorophyll concentration;  $g_t$ : total conductance to CO<sub>2</sub> between the leaf surface and carboxylation sites ( $1/g_t = 1/g_s + 1/g_m$ ). Multiple regression from  $V_{cmax}$  and  $J_{max}$  to  $A_{n-g}$  was used to construct photosynthetic capacity (PC) as a component variable (hexagonal frame). The SEM (using psem function in piecewiseSEM package R) of biomass and  $A_{n-g}$  in wintersweet by biomass (a) and by  $A_{n-g}$  (b). Arrows mean the directional influence between the variables and the solid lines represent significant relationships, and the dashed lines refer to nonsignificant relationships ( $P > 0.05$ ). The numbers near the arrows represent the standardized path coefficients (for continuous variables), and the numbers under the box with  $R^2$  refer to the degree of variation of the variable interpreted by all paths. Curved double arrows represent a significant correlation between variables (with correlation coefficient). The values on the line from the categorical variable indicated the continuous variable estimated marginal means by the treatment levels.

of  $g_m$  and more than 50% of the limitation to photosynthesis was attributable to stomatal conductance, which is very high compared to other tree species (Sakoda et al., 2021). The results of the relative

limitation analysis of photosynthesis further corroborated this conclusion. Furthermore, the results of the structural equation model indicate that CO<sub>2</sub> conductivity had a direct effect on  $A_{n-g}$ , and the influence coefficient was 0.61 high, further confirming that the photosynthesis of Wintersweet was mainly limited by the resistance to CO<sub>2</sub> diffusion (Figure 6). Elevated CO<sub>2</sub> further increased the proportion of stomatal limitation to photosynthesis in wintersweet. The results suggest that wintersweet is a very conservative species for water use and its water use efficiency will likely be further enhanced by elevated CO<sub>2</sub> in the future. The high-water use efficiency is a highly desirable trait for landscaping trees.

## 5 | CONCLUSIONS

As a popular and special landscape tree species, wintersweet plays an important role in urban landscapes, particularly for the winter season. The unique fresh floral scent of its yellow flowers makes people feel magical and quiet in the cold winter. Its high drought resistance may be related to its low  $g_s$ . A lower  $g_s$  has a greater limitation to transpiration than to photosynthesis, enhancing water use efficiency. However, the increase in leaf area (canopy) under elevated CO<sub>2</sub> indicates that the species may have increased growth in the future. The LES with elevated CO<sub>2</sub> showed a decrease in SLA and an increase in  $N_{area}$ , indicating that future climate conditions may be favourable for the growth and stress resistance of wintersweet. Wintersweet exhibited typical symptoms of photosynthetic acclimation, such as decreased PC in response to elevated CO<sub>2</sub>. However, leaf nitrogen concentration increased, indicating that Wintersweet may be more sensitive to future climate change and soil nitrogen levels.

We proposed and tested the framework to use a combination of LES and photosynthetic acclimation to evaluate the potential performance of Wintersweet under future CO<sub>2</sub>. The results suggest that wintersweet should be cultivated more in future urban landscape planning, and nitrogen fertilization should further enhance growth and physiological performance under the predicted future CO<sub>2</sub> levels. Our results suggest that elevated CO<sub>2</sub> can further enhance the water conservation and water use efficiency of wintersweet in the future, making it a highly desirable species for landscaping in the future when more frequent and more severe drought spells are predicted under the scenario of climate change.

## AUTHOR CONTRIBUTIONS

Lei Wang: Conceptualization, Methodology, Data curation, Writing – original draft. Qing-lai DANG: Conceptualization, Writing – review & editing.

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## CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known competing financial interests of personal relationships that could have appeared to influence the work reported in this paper.

## DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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