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Effects of Nitrogen Supply on the Physiological and Morphological Responses to Elevated [CO_2] in Yellow Birch (*Betula alleghaniensis* Britt.)

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Abstract

Climate change impacts soil nitrogen, influencing plant responses to elevated atmospheric [CO_2]. Understanding the interaction between nitrogen supply and elevated [CO_2] is crucial for predicting plant future performance. This study examined the interactive effects of elevated [CO_2] and nitrogen supply on the eco-physiological performance of yellow birch. Seedlings were exposed to two [CO_2] levels and five nitrogen supply levels for 4 months. Growth parameters such as seedling height and root collar diameter increased with higher nitrogen supply and elevated [CO_2], while specific leaf area decreased. [CO_2] elevation and increasing nitrogen supply also increased the total and stem, and leaf biomass. The elevated [CO_2] increased the stem mass ratio but decreased the root-to-shoot ratio and root mass ratio. However, decreases in nitrogen supply increased root mass ratio and root-to-shoot ratio. The elevated [CO_2] increased the maximum rate of Rubisco carboxylation (V_{cmax}) and photosynthetic electron transport (J_{max}), but the effect on J_{max} was statistically significant only at the two highest nitrogen supply levels. The results indicate that yellow birch may increase photosynthetic capacity, biomass, and growth in the future when [CO_2] is higher.

Keywords

Climate Change, Yellow Birch (*Betula alleghaniensis* Britt.), Elevated [CO_2], Soil Nitrogen Availability, Growth, Biomass, Photosynthesis

1. Introduction

Continued increases in atmospheric carbon dioxide (CO_2) and other greenhouse gases will continue to cause long-lasting adverse effects on global climate, such as rising global temperatures and altered precipitation patterns [1]. These climate changes can also influence environmental factors, including soil nitrogen availability, ultimately altering plant and ecosystem productivity [2] [3]. The burning of fossil fuels has substantially increased atmospheric nitrogen deposition into soil over the last century and the increase is expected to continue in the foreseeable future [4]-[6]. Furthermore, climate change can modify soil nitrogen availability by affecting litterfall and litter decomposition rates in forests [2].

Elevated [CO_2] generally increases photosynthesis and plant growth, but these responses depend on site conditions, such as soil nitrogen (N) availability [7]-[10]. Soil nitrogen is a critical component of photosynthetic enzymes, making soil nitrogen availability a key regulator of plant responses to elevated [CO_2] [11]. Elevated [CO_2] can affect soil nitrogen concentration by influencing plant growth and nitrogen uptake. When plants grow vigorously, their demand for nitrogen increases [12] [13]. Moreover, elevated [CO_2] can also affect soil nitrogen by influencing the amount and quality of litter and its decomposition [14]-[17].

Photosynthesis is a primary physiological process through which nitrogen supply affects plants [8] [18] [19]. Elevated [CO_2] enhances photosynthesis by increasing Rubisco carboxylation rates and substrate supply, while suppressing Rubisco oxygenation [20]-[23]. However, elevated [CO_2] can cause the downregulation of photosynthetic machinery as demonstrated in both FACE and controlled-environment experiments [24] [25]. Photosynthetic downregulation has been reported for many plant species grown under limited nitrogen availability and elevated [CO_2] [26]-[31]. This downregulation is often linked to tissue nitrogen dilution caused by excessive carbohydrate accumulation under elevated [CO_2], which reduces the mass based leaf nitrogen concentration [32]-[34]. Also, the excessive accumulation of nonstructural carbohydrates suppresses the expression of genes for Rubisco synthesis [35] [36]. However, some studies have found no correlation between photosynthetic downregulation and leaf nitrogen concentration or nitrogen supply, highlighting the complexity of these interactions [37] [38]. Other studies have found that plants increase nitrogen allocation to roots at the expense of above-ground organs under elevated [CO_2] [39]-[42]. Thus, a good understanding of how nitrogen supply affects the physiological and morphological responses of plants to elevated [CO_2] is critical for predicting the performance of plants and plant communities under future climate conditions [43]. Moreover, elevated [CO_2] can reduce nitrate assimilation in the leaf by reducing photorespiration, which in turn will increase plant nutrient demand and may result in the eventual depletion of the nutrient pool in the soil. If the plant is not efficiently assimilating nitrate, it might compensate by increasing its nutrient uptake from the soil, creating a higher demand, which will result in the depletion of nutrient pools in the soil over time, affecting the overall nutrient balance [44]-[47].

Yellow birch (*Betula alleghaniensis Britt.*) is a deciduous tree species native to North America with a medium growth rate [48]. It is highly valued both ecologically and commercially. As a hardwood species, it is prized for its heavy, strong, and close-grained wood, making it a significant source of lumber for quality products such as furniture, cabinetry, interior finishes, veneers, tool handles, boxes, woodenware, interior doors, charcoal, and pulp [49] [50]. Additionally, it serves as an important food source for both livestock and wildlife [50]. Beyond its commercial uses, yellow birch also contains bioactive compounds with promising applications in the food, pharmaceutical, and cosmetic industries [51]. Its ecological importance is equally noteworthy. As an early colonizer, yellow birch has been observed to play a key role in rehabilitating disturbed areas, such as sites damaged by brine from well-injection fluids. Its ability to establish itself as soil salinity levels return to near-normal demonstrates its potential for ecosystem recovery [52]. However, yellow birch is highly sensitive to environmental and climatic changes, facing significant challenges such as high mortality rates under drought and freeze-thaw conditions [53] [54]. Its shallow root system further limits adaptability, contributing to its vulnerability in degraded forest stands and under global environmental changes [55]. While yellow birch demonstrates physiological and morphological responses to environmental shifts, studies on these responses are inconsistent or contradictory. For example, Song and Cheng [53] report that elevated CO_2 increases biomass allocation to roots, while Wang *et al.* [31] find elevated CO_2 reduces biomass allocation to roots. Its responses to CO_2 are affected by other environmental factors, such as soil moisture [56]. While there are numerous studies investigating the effect of nitrogen supply on the responses of other birch species to elevated CO_2 in recent years, For instance, elevated CO_2 and increasing nitrogen supply synergistically enhance the photosynthesis and biomass production of white birch [57]-[60]. Wang *et al.* [30] report that a higher nitrogen supply reduces the scope of photosynthetic downregulation induced by elevated CO_2 and warmer temperatures in *B. costata*. However, there is no such information in the literature on *Betula alleghaniensis*. In this study, we investigated the interactive effects of CO_2 and nitrogen supply on the physiological and morphological performance of *Betula alleghaniensis.* Since our experimental protocols are similar to those of [31], we hypothesized that the responses of *Betula alleghaniensis* to CO_2 and nitrogen supply would be similar to those of *B. costata*, *i.e.*, elevated CO_2 would lead to photosynthetic downregulation and the scope of the downregulation would be smaller under higher nitrogen supply, and elevated CO_2 and higher nitrogen supply would both tree growth and biomass production but reduce biomass allocation to roots.

2. Materials and Methods

2.1. Plant Material and Experimental Design

The experiment was conducted in the Lakehead University Forest Ecology Complex (Thunder Bay, On., Canada). Yellow birch seeds (*B. alleghaniensis* Britt.) were obtained from the National Tree Seed Center Fredericton, New Brunswick, Canada (seed origin: 47.45˚N, −67.45˚W). Seeds were stratified at 4˚C for three weeks and then sown in horticultural trays filled with a mixture of peat moss and vermiculite (2:1, v/v). The day/night temperature and photoperiod during germination were set to 25/16˚C and 16 h, respectively. Seedlings of relatively uniform size (2 cm average height) were transplanted into pots (14 cm height × 13 cm square) filled with peat moss and vermiculite (2:1, v/v) 10 days after the completion of germination.

The treatments were comprised of two [CO_2 (ambient 400 $\mu mol \cdot mol^{-1}$ versus elevated 1000 $\mu mol \cdot mol^{-1}$ (predicted level for the end of the century by [1]) and five nitrogen levels (25, 50, 100, 150, and 200 $mg \cdot N \cdot L^{-1}$). The elevated [CO_2] treatment level (1000 $\mu mol \cdot mol^{-1}$) is consistent with a representative concentration pathway (RCP) 8.5 scenario adopted by Intergovernmental Panel on Climate Change ([1]), where the current high rate of [CO_2] emission into the atmosphere is predicted to continue and the atmospheric [CO_2] will reach >1000 $\mu mol \cdot mol^{-1}$ in the year 2100. These levels represent current conditions and a realistic future scenario under continued emissions, allowing the study to assess how yellow birch may respond to future elevated [CO_2] environments. The phosphorus and potassium concentrations were 60 and 150 $mg \cdot L^{-1}$, respectively, for all the nitrogen treatments. The highest and lowest nitrogen (N) concentrations were slightly above and below, respectively, the values typical of nutrient-rich and nutrient-poor sites for the species, representing the range of soil N found in the species' natural habitats. [30] [31] [61] [62]. The seedlings were fertilized once a week (100 ml per plant).

The experiment was carried out using a split-plot design. The [CO_2] treatment (main plot) was randomly allocated to four independent greenhouses of identical design (dimension: 6 m × 6.5 m) (2 independent replicates per [CO_2]). The five nitrogen treatments were applied to subplots within each greenhouse and the physical location of each treatment was randomized. There were ten seedlings in each treatment combination (a total of 200 seedlings: 2 CO_2 × 2 replicates × 5 N × 10 seedlings). Individual seedlings were spaced far enough from each other to avoid mutual shading.

The [CO_2] elevation was achieved using CO_2 generators (model GEN-2E; Custom Automated Products Inc., Riverside, California, USA). The temperature and photoperiod settings were adjusted weekly to emulate the diurnal and seasonal patterns at the seed origin. The environmental conditions (photoperiod, air temperature, [CO_2], and humidity) in all the greenhouses were monitored and controlled automatically by an Argus Titan Environment-control system (Argus Control Systems Ltd, Vancouver, BC, Canada). The temperature and photoperiod set values were derived from the 3-year weekly averages of Environment Canada-2019 records for the seed origin. The average temperatures were 21˚C ± 1˚C (day) and 13˚C ± 1˚C (night) and 50% humidity. The daily minimum temperature in each greenhouse occurred between 3.00 a.m. and 6.00 a.m. After 6.00 a.m., the temperature increased every three hours until it reached the maximum temperature at 12.00 p.m. The maximum temperature was held for 6 hours (12.00 p.m. to 6.00 p.m.) and then decreased every three hours till 3.00 a.m. the next morning. High-pressure sodium lamps (P. L. Systems) were used to extend the natural photoperiod to set values when the natural day-length shorter than required or when PAR flux density was below 500 μmol·m^{-2}·s^{-1}. The lamps provided about 600 μmol·m^{-2}·s^{-1} PAR at the seedling canopy level (with less blue light than sunlight but a similar R/FR ratio). Mean daily light integral was 25 - 30 mol·m^{-2} day^{-1}. The volumetric moisture content of the growing medium was maintained at 40% - 50% as measured with a HH$_2$ Moisture Meter (Delta-T Devices, Cambridge, UK). The experiment emulated the natural environment conditions of a growing season (June 4th to September 30th).

2.2. Foliar Gas Exchange Measurements

Foliar gas exchange was measured using a PP-Systems CIRAS-3 open gas exchange system with PLC3 Universal Leaf Cuvette (PP Systems, Amesbury, MA, USA) after 60 days of treatments. Three seedlings from each treatment combination were randomly selected for the measurements. A healthy and fully expanded leaf (2nd mature leaf from the top, 30 days after leaf opening) was measured under the following conditions: 22˚C air temperature, 50% relative humidity, 800 μmol·m^{-2}·s^{-1} PAR (measured saturation PAR: 600 μmol·m^{-2}·s^{-1}), and sequentially at 400, 40, 20, 40, 60, 80, 100, 150, 200, 300, 400, 500, 700, 1000, 1100, 1400 and 1600 μmol·mol^{-1} CO$_2$ for the ambient [CO$_2$] treatment and sequentially at 1000, 40, 20, 40, 60, 80, 100, 150, 200, 300, 400, 500, 700, 1000, 1100, 1400 and 1600 μ·mol·mol^{-1} CO$_2$ for the elevated [CO$_2$] treatment. The measurements were carried out between 7:00 a.m. and 3:00 p.m. when our tests showed relatively stable gas exchange measurements. The net photosynthetic rate at elevated [CO$_2$] (P_{n1000}) and P_n at the ambient [CO$_2$] (P_{n400}) were extracted the A/Ci data for each sample tree. The corresponding stomatal conductance (g_s), transpiration rate (E), and instantaneous water-use efficiency (iWUE) were extracted from measurements performed respectively at 400 μmol·mol^{-1} for ambient [CO$_2$] and 1000 μmol·mol^{-1} for elevated [CO$_2$] for statistical analysis. The sequence of measurements among different treatments was randomized to avoid systematic errors.

2.3. Growth, Biomass, and Biomass Allocation

All the seedlings were measured for total height and root-collar diameter. Five mature leaves were selected from each seedling for specific leaf area measurement using a Win Folia system (Regent Instrument Inc., Canada). The seedlings were then harvested, roots were washed and oven-dried at 70˚C for 48 h. The dry mass of foliage, roots, and stems was measured separately on an electronic balance. The dry mass of the leaves for the specific leaf area measurement was measured separately from other leaves for the determination of specific leaf area (SLA = leaf area/leaf dry mass). The following biomass allocation parameters were calculated: leaf mass ratio (LMR = leaf dry mass/seedling dry mass), stem mass ratio (SMR = stem dry mass/total seedling dry mass), root mass ratio (RMR = root dry mass/total seedling dry mass) and root-to-shoot ratio (RSR = root dry mass/(leaf + twigs + branches+ stem dry mass)).

2.4. A/Ci Curve Fitting

A biochemical model of photosynthesis was used to derive photosynthetic parameters from each set of gas exchange measurements [63]. The parameters estimated were the potential maximum rate of Rubisco carboxylation (V_{cmax}) and the potential maximum rate of electron transport for RuBP regeneration under saturating light (J_{max}). The model was fit using the "default" fitting method of the "fitaci" function of the "plantecophys" package [64] of R software package 4.2.2 (R Development Core Team 2023). Assimilation rate (μmol·CO_2·m^{-2}·s^{-1}), sub-stomatal CO_2 concentration (μmol·mol^{-1}), leaf temperature (˚C) and PAR_i (μmol·m^{-2}·s^{-1}) were used to fit the Farquhar model.

2.5. Data Analysis

The data were examined graphically for the normality of distribution (probability plots of residuals, Shapiro-Wilk normality test) and homogeneity of variance (scatter plots) before being subjected to the analysis of variance (ANOVA). The effects of [CO_2] and nitrogen were considered as "fixed effect" in the ANOVA. The full model used was:

$$Y_{ijk} = \mu + \alpha_i + \eta_{k(i)} + \beta_j + (\alpha\beta)_{ij} + \varepsilon_{ijk}$$

Where, μ = overall mean, α_i = fixed effect of CO_2 treatment-whole plot factor (i = 1, 2), β_j = fixed effect of nitrogen treatment-split plot factor (j = 1, 2, 3, 4, 5), $(\alpha\beta)_{ij}$ = corresponding interaction term, $\eta_{k(i)}$ = whole plot error, ε_{ijk} = split plot error.

An effect was considered significant if $P \le 0.05$. When ANOVA showed a significant ($P \le 0.05$) interaction or a significant nitrogen effect, Fisher's Least Significant Difference (LSD) post hoc test was used to compare individual means. The sample size in this study was relatively small, which increased the likelihood of real treatment effects being undetected (type II) error. LSD post-hoc test reasonably controls type II error for split plot design in this experiment. All the analyses were performed using R studio (Version 4.2.2, R Development Core Team 2023).

3. Results

3.1. Growth

[CO_2] and nitrogen supply exhibited significant interactive effects on seedling height growth, root collar diameter growth (RCD), and specific leaf area (SLA) (**Table 1**). While seedling height generally increased with increasing nitrogen treatment in both [CO_2] treatments, the difference in height was not statistically significant between the two highest nitrogen levels in seedlings grown under elevated [CO_2] (**Figure 1(a)**). Elevated [CO_2] significantly increased seedling height growth only under the 150 mg·N·L^{-1} nitrogen treatment (average increase by 4.31%) (**Figure 1(a)**). In contrast, the elevated [CO_2] increased RCD in all the nitrogen treatments (average increase 18%) but the increases at the two lowest nitrogen treatments were not statistically significant (**Figure 1(b)**). Seedling RCD generally increased with increasing nitrogen supply in both ambient and elevated $[CO_2]$, but the increases were generally greater under elevated than ambient $[CO_2]$ (by 18.12%), particularly at higher nitrogen levels (100, 150 and 200 $mg \cdot L^{-1}$, **Figure 1(b)**). The SLA generally declined with increases in nitrogen supply, but not all the differences between two adjacent levels of nitrogen supply were statistically significant (**Figure 1(c)**). The elevated $[CO_2]$ significantly reduced SLA across all nitrogen treatments (average reduction 24.3%, **Figure 1(c)**).

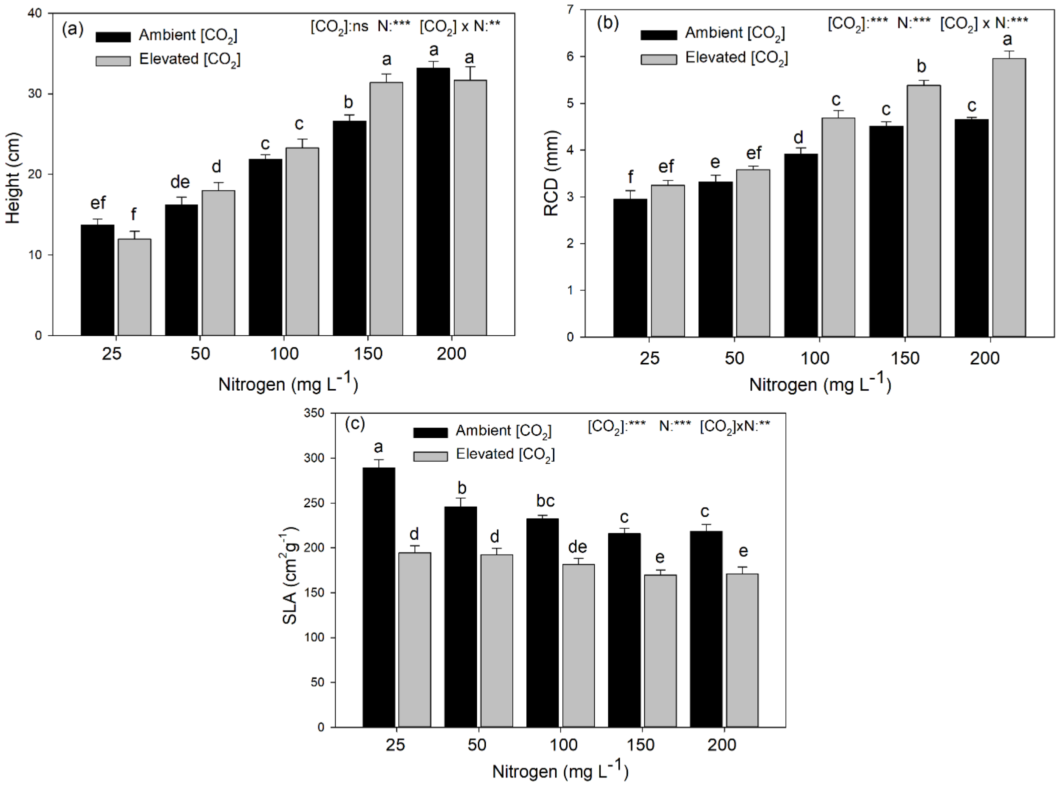


Figure 1. Mean (+SE), (a) height growth, (b) RCD, (c) SLA (n = 5) of yellow birch seedlings grown under two levels of $[CO_2]$, five levels of nitrogen supply for 4 months. Means with different letters are significantly different from each other based on Fisher's least significant difference post hoc test ($p < 0.05$). The significance of main effects and interactions are indicated as: ns, not significant; and $^{*}p < 0.05$; $^{**}p < 0.01$; and $^{***}p < 0.001$ are indicated on the top of each graph.

Table 1. Summary of ANOVA (*P*-value, F value and Degree of freedom (DF)) results for height, RCD, and SLA of yellow birch seedlings. The numbers in bold font are statistically significant ($P \leq 0.05$). Note: C: $[CO_2]$, N: Nitrogen, C × N: $[CO_2]$ and nitrogen interaction.

Variable	C (DF = 1)	N (DF = 4)	C × N (DF = 4)
		Height	
F	2.659	150.831	4.11
P	0.106	<0.001	0.0042
		Root collar diameter	
F	77.633	112.307	6.013

Continued

P	<0.001	<0.001	<0.001
	Specific leaf area		
F	149.297	14.275	3.669
P	<0.001	<0.001	0.0082

3.2. Biomass and Biomass Allocation

Root, stem, leaf and total biomass all increased with increasing nitrogen supply, but the difference between 25 and 50 mg·L^{-1} N and that between 150 and 200 mg·L^{-1} N were not statistically significant (Figure 2). The elevated [CO$_2$] significantly increased total seedling biomass (by 15.95%), stem biomass (31.36%), leaf biomass (19.89%), and root biomass (6.11%), but the effect on root biomass was not statistically significant (Figure 2, Table 2).

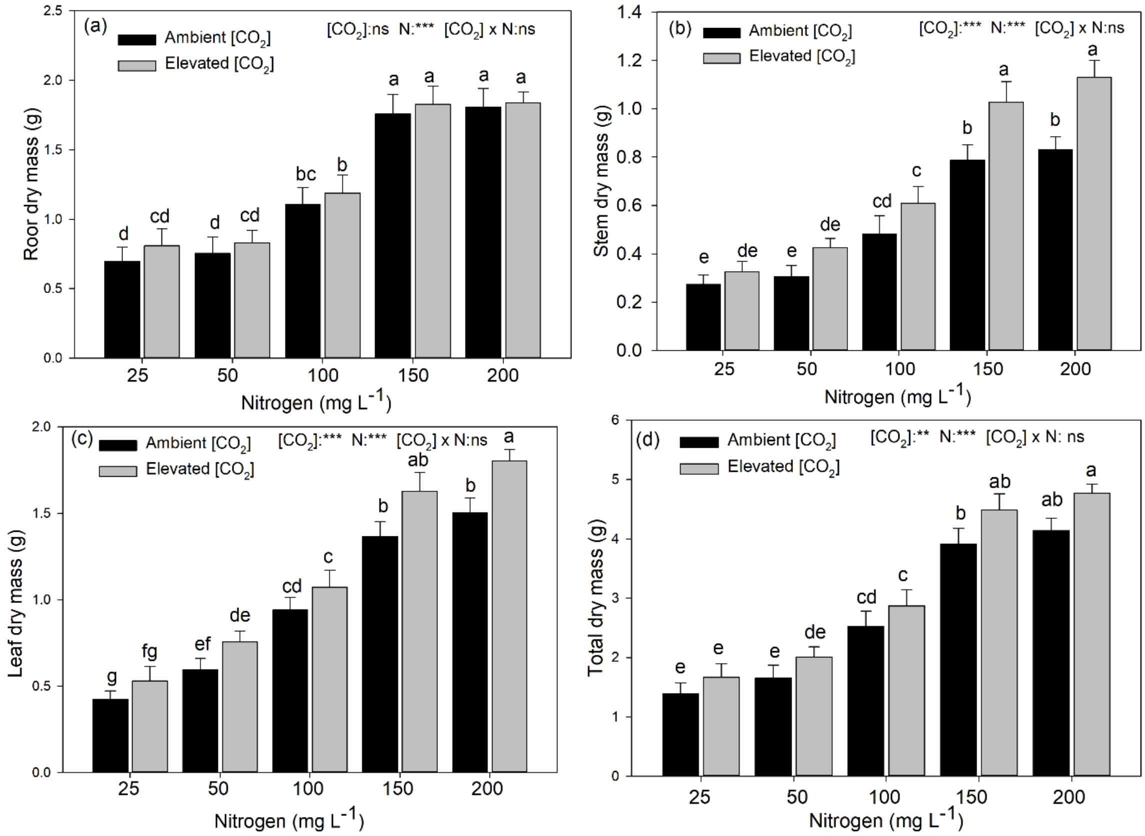


Figure 2. Mean (+SE), biomass of yellow birch seedlings grown under two levels of [CO$_2$], five levels of nitrogen supply for 4 months. Data are pooled across [CO$_2$] and nitrogen for (a), (b), (c), (d) (n = 100): five seedlings with two replications per treatment, two levels of [CO$_2$], five levels of nitrogen 5 × 2 × 5 × 2 = 100). Means with different letters are significantly different from each other based on Fisher's least significant difference post hoc test ($p < 0.05$). The significance of main effects and interactions are indicated as: ns, not significant; and $^*p < 0.05$; $^{**}p < 0.01$; and $^{***}p < 0.001$ are indicated on the top of each graph.

RSR (0.955) and RMR (0.478) were significantly greater in the lowest nitrogen supply (25 mg·N·L^{-1}) than in other nitrogen treatments and were not significantly different among other nitrogen levels (**Figure 3(a, c)**, **Table 3**). In contrast, the LMR was significantly smaller in the lowest nitrogen treatment (0.322) than other nitrogen levels (**Figure 3(b)**). The elevated [CO_2] significantly decreased RSR (by 11.39%) and RMR (by 6.57%), but significantly increased SMR (by 13.51%) (**Figure 3(a, c, d)**, **Table 3**).

Table 2. Summary of ANOVA (*P*-value, F value and Degree of freedom (DF)) results for root, leaf, stem, and total dry mass of yellow birch seedlings. The numbers in bold font are statistically significant ($P \leq 0.05$). Note: C: [CO_2], N: Nitrogen, C × N: [CO_2] and nitrogen interaction

Variable	C (DF = 1)	N (DF = 4)	C × N (DF = 4)
		Root DM	
F	1.219	47.615	0.037
P	0.272	<0.001	0.997
		Leaf DM	
F	12.889	83.969	0.230
P	<0.001	<0.001	0.92061
		Stem DM	
F	20.346	55.469	1.431
P	<0.001	<0.001	0.230
		Total DM	
F	10.301	78.024	0.267
P	0.0018	<0.001	0.8984

Table 3. Summary of ANOVA (*P*-value, F value and Degree of freedom (DF)) results for LMR, SMR, RMR, RSR of yellow birch seedlings. The numbers in bold font are statistically significant ($P \leq 0.05$). Note: C: [CO_2], N: Nitrogen, C × N: [CO_2] and nitrogen interaction.

Variable	C (DF = 1)	N (DF = 4)	C × N (DF = 4)
		LMR	
F	0.185	4.577	0.088
P	0.6682	0.00208	0.98583
		SMR	
F	15.972	1.841	0.389
P	<0.001	0.1281	0.81599
		RMR	
F	6.795	4.875	0.402
P	0.01072	0.00133	0.807
		RSR	
F	6.826	5.927	0.250
P	0.0105	<0.001	0.9091

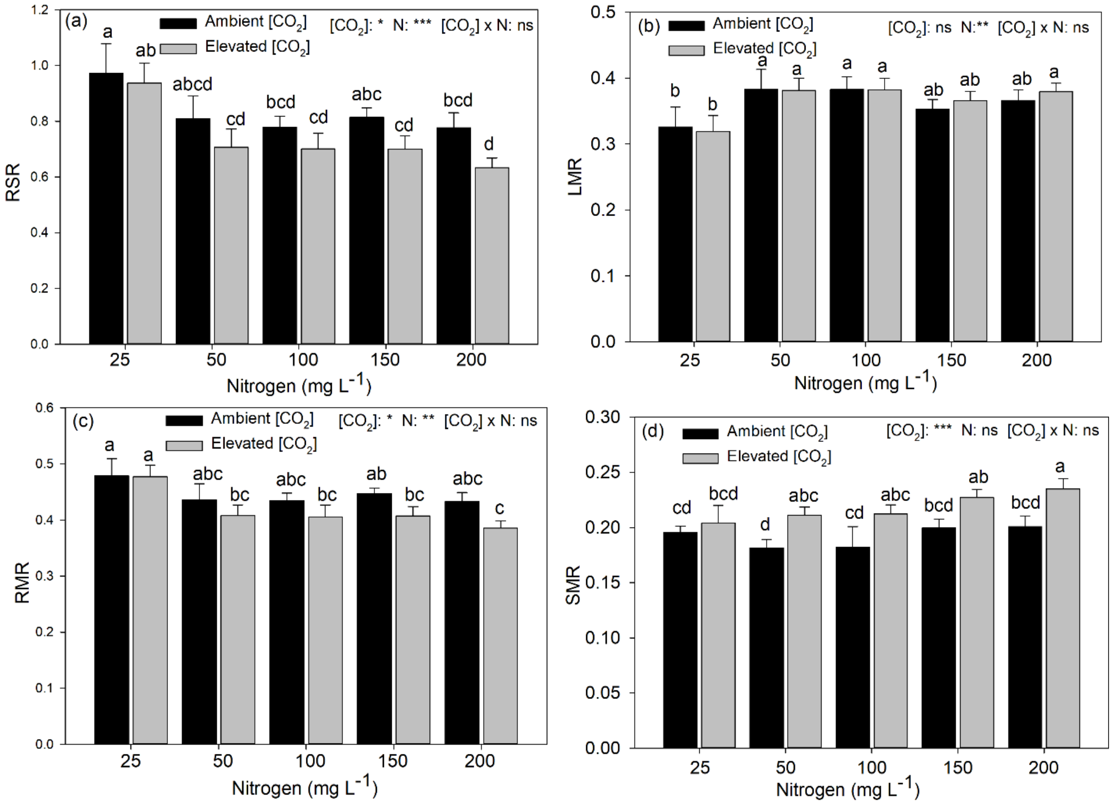


Figure 3. Mean (+SE) biomass allocation of yellow birch seedlings grown under two levels of [CO_2], five levels of nitrogen supply for 4 months. Data are pooled across [CO_2] and *nitrogen* for (a), (b), (c), (d) (n = 100): five seedlings with two replications per treatment, two levels of [CO_2], five levels of nitrogen 5 × 2 × 5 × 2 = 100). Means with different letters are significantly different from each other based on Fisher's least significant difference post hoc test ($p < 0.05$). The significance of main effects and interactions are indicated as: ns, not significant; and $^*p < 0.05$; $^{**}p < 0.01$; and $^{***}p < 0.001$ are indicated on the top of each graph.

3.3. Foliar Gas Exchange

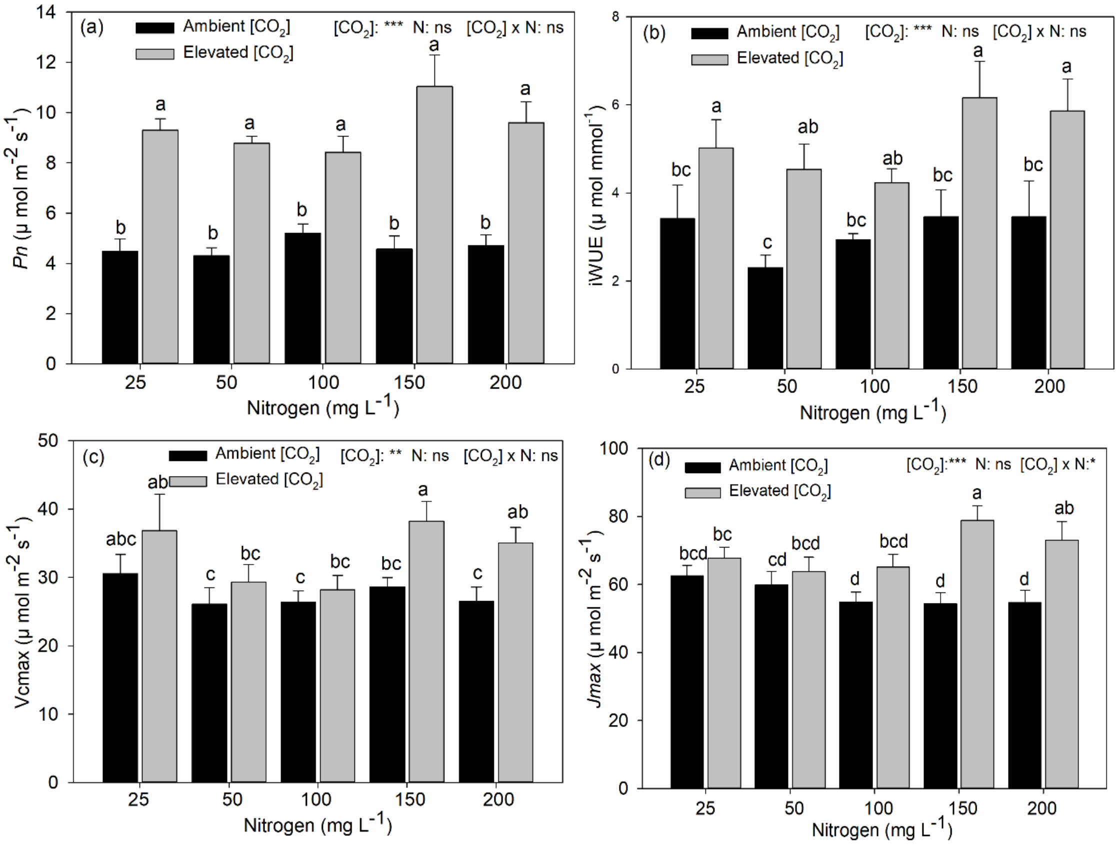
Table 4. Summary of ANOVA (P-value, F value and Degree of freedom (DF)) results for P_n, g_s, E, iWUE, V_{cmax}, J_{max} of yellow birch seedlings. The numbers in bold font are statistically significant ($P \le 0.05$). Note: C: [CO_2], N: Nitrogen, C × N: [CO_2] and nitrogen interaction.

Variable	C (DF = 1)	N (DF = 4)	C × N (DF = 4)
		P_n	
F	167.405	0.494	1.423
P	<0.001	0.740	0.240
		g_s	
F	0.917	1.178	0.800
P	0.343	0.332	0.531
		E	
F	3.551	0.917	0.222
P	0.0655	0.4617	0.9250

Continued

		iWUE	
F	36.403	1.791	0.435
P	<0.001	0.146	0.783
		V_{cmax}	
F	11.404	2.448	0.743
P	0.00144	0.05856	0.56739
		J_{max}	
F	25.523	0.912	2.555
P	<0.001	0.4642	0.0476

Elevated [CO$_2$] significantly increased the light saturated P_n (9.43 μ·mol·m^{-2}·s^{-1} vs. 4.65 μ·mol·m^{-2}·s^{-1}) and *iWUE* (by 65.71%) (Figure 4(a, b), Table 4). Neither [CO$_2$] nor nitrogen supply significantly affected g_s or E (Table 4). The elevated [CO$_2$] significantly increased both V_{cmax} (by 21.22%) (Figure 4(c)) and J_{max} (by 21.80%) (Figure 4(d)) and there was an interactive effect of [CO$_2$] and nitrogen on J$_{max}$: J_{max} was significantly higher in the two highest nitrogen treatments in seedlings grown under the elevated [CO$_2$] (150 mg·L^{-1}: 78.88 μmol·m^{-2}·s^{-1}, 200 mg·L^{-1}: 73.07 μmol·m^{-2}·s^{-1}), but nitrogen treatment had no significant effect on J_{max} in the ambient [CO$_2$] treatment (Figure 4(d)).



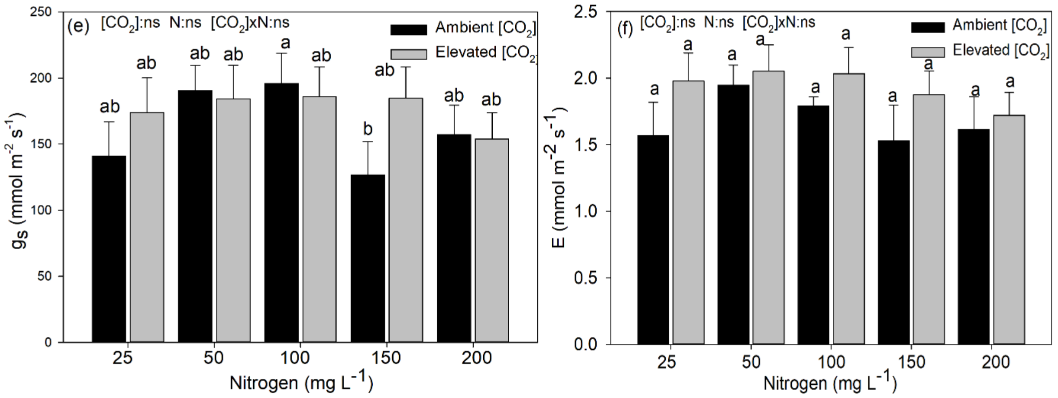


Figure 4. Mean (+SE) (a) P_n, (b) *iWUE*, (c) V_{cmax}, (d) J_{max}, (e) g_s, (f) E of yellow birch seedlings grown under two levels of [CO_2], five levels of nitrogen supply for 4 months. Data are pooled across [CO_2] and nitrogen for (a), (b), (c), (d), (e), (f) (n = 60): three seedlings with two replications per treatment, two levels of [CO_2], five levels of nitrogen $3 \times 2 \times 5 \times 2 = 60$). Means with different letters are significantly different from each other based on Fisher's least significant difference post hoc test ($p < 0.05$). The significance of main effects and interactions are indicated as: ns, not significant; and $*p < 0.05$; $**p < 0.01$; and $***p < 0.001$ are indicated on the top of each graph.

4. Discussion

The elevated [CO_2] increased seedling root collar diameter growth and shoot biomass, and the increases were greater with higher nitrogen supplies. These synergistic effects were also shown seedling height growth (150 mg·N·L^{-1} nitrogen vs. lower levels). These results support our hypothesis that the stimulation of growth by elevated [CO_2] would be higher with increasing N supply. The results are in general agreement with [58] on white birch (*B. papyrifera* Marsh.) and [31] on yellow birch *B. costata*. The synergistic effects may be attributable to the increases in nitrogen use efficiency by elevated [CO_2] [65]-[67]. Increases in aboveground growth by elevated [CO_2] are common in the literature [68] [69]. However, while the lack of significant positive effect of elevated [CO_2] on height growth in this study is consistent with the findings for some other tree species such as *Eucalyptus miniata* [70] and *Populus* [71], explanations are needed. Height growth is a key trait determining the competitiveness of plants in aboveground competition [72] [73] and has a higher priority in carbohydrates allocation than diameter growth and defense and stress resistance [74]. Therefore, if the need of carbohydrates for height growth is satisfied under the ambient [CO_2], [CO_2] elevations will not future increase height growth.

Growth is generally positively correlated with specific leaf area (SLA) in trees [75]-[78]. However, the elevated [CO_2] treatment in this study significantly reduced specific leaf area (SLA) of yellow birch in all the nitrogen treatments. Similar results have been reported for white birch [58], barley and tomato plants [79]. The reduction in specific leaf area (SLA) by elevated [CO_2] was most likely the result of increased carbohydrates accumulation rather than changes in leaf structure or anatomy [80] [81].

Both elevated [CO_2] and increasing nitrogen (N) supply increased the stem dry mass, leaf dry mass and total dry mass of yellow birch. These results are consistent with the findings of several other studies [31] [56] [58] [82] [83]. Although plants generally downregulate their photosynthetic capacity in response to elevated [CO_2], the actual rates of photosynthesis generally increase, leading to an increase in biomass production and growth [84]. Increases in photosynthesis and biomass production under increased nitrogen supply are generally related to increases in nitrogen allocation to photosynthetic apparatus and subsequent increases in carbohydrate production [85]-[87]. The synergistic effects of elevated [CO_2] and higher nitrogen supply, as found in this and other studies (*e.g.*, [88] [89]), are attributable to the increase of nitrogen use efficiency under elevated [CO_2] [65]-[67]. Effects of elevated [CO_2] on root biomass, however, are highly variable: from no effects in this study to increases in [90]. These contrasting responses of roots to elevated [CO_2] appear to be related to genetic differences [90]. Nonetheless, our results indicate that yellow birch growing on rich sites will likely benefit more from the continued elevation of [CO_2] than their counterparts on poor sites.

The response of biomass allocation to elevated [CO_2] varies among different studies. Stem mass ratio (SMR) increased in response to elevated [CO_2] in this and some other studies [91] [92]. [88] report elevated [CO_2] stimulates the stem diameter growth of *Larix sibirica*. [81] suggest that elevated [CO_2] increases stem biomass density. Some older studies, in contrast, find not significant [CO_2] effect on biomass allocation between roots and shoots [93]-[96]. The differences in the response may be attributable to differences in other environmental factors, such as nitrogen supply. This and other studies [97]-[99] find that [CO_2] and nitrogen supply interactively affect biomass allocations in trees. The results that elevated [CO_2] reduced biomass allocation to roots and the reduction was greater under higher nitrogen supply are consistent with the findings of [31] [100]. The results are also in agreement with the results of long-term FACE studies that elevated [CO_2] has greater positive effects on aboveground growth than roots under higher nitrogen supply [24] [89] [101]. The consistent findings of short-term controlled environment studies and long-term field research indicate that trees growing on nutrient-rich sites will benefit more from elevated [CO_2] than those growing on poor sites and that fertilization in the future under elevated [CO_2] will be more effective in increasing forest productivity. Additionally, elevated [CO_2] can reduce nitrate assimilation in leaves by suppressing photorespiration, a process critical for converting nitrate into organic forms within the plant. This reduction in nitrate assimilation, combined with increased growth and biomass production stimulated by elevated [CO_2], significantly raises overall nutrient demand, particularly for nitrogen. The increased nutrient demand may lead to compensatory uptake of soil nutrients, potentially depleting soil nutrient pools over time, which in turn can alter the biomass allocation between aboveground and below-ground organs due to variations in soil nitrogen availability [102]. While these results indicate that the performance of seedlings can serve as a reliable indicator of tree's response [103], this and other controlled environment studies do have limitations, for example, they do not capture the full complexity of natural ecosystems or the fluctuations of environmental conditions at nature sites. Therefore, cautions should be exercised when applying the results from controlled environment studies to the field or even computer modeling.

It is interesting to note that elevated [CO_2] increased photosynthesis, but N supply had no significant effect on photosynthetic rates in yellow birch in this study. In response to the elevation of [CO_2], the photosynthetic rate of yellow birch was more than doubled. However, the photosynthetic rates were relatively stable among different levels of nitrogen supply. In contrast, the total leaf biomass per tree increased linearly with increases in nitrogen supply. These results suggest that the primary mechanism of response to variation in nitrogen supply in yellow birch was morphological rather than physiological. This conclusion is consistent with that [30]. Our findings suggest that it is critically important to assess different mechanisms of responses in order to obtain the whole picture of the tree's response. Furthermore, it is interesting to note there are large variations in measured photosynthetic rates of *B. Allegheniensis* among different studies. For example, [30] report 20 $\mu mol \cdot m^{-2} \cdot s^{-1}$ under elevated [CO_2], it varies from 7 to 12 $\mu mol \cdot m^{-2} \cdot s^{-1}$ under elevated [CO_2] and from about 7 to 9 $\mu mol \cdot m^{-2} \cdot s^{-1}$ under ambient [CO_2] in [56] while the rate ranged from about 5 $\mu mol \cdot m^{-2} \cdot s^{-1}$ under ambient [CO_2] to about 11 $\mu mol\ m^{-2} \cdot s^{-1}$under elevated [$CO_2$] in this study. The large differences appear to be related to seed source, temperature and soil moisture. Although the three studies use the same species, the seeds are from very different geographic locations. The growth temperatures in [30] [56] are much higher than the values in this study. [30] used 25/16˚C day/night temperature for ambient [CO_2] treatment and 29/20˚C for elevated [CO_2] treatment while [56] used 26/19˚C day/night temperature for both ambient and elevated [CO_2]. We emulated the day and seasonal (June 4th to September 30th) temperatures of the seed source site throughout the entire experiment and the actual temperatures (21/13˚C day/night average) were several degrees lower than the other two studies and varied with time of day and from week to week. The temperature that we used to measure photosynthesis was also much lower than the other two studies. Besides the direct temperature effects, soil moisture could also have an indirect effect. Under similar irrigation schemes, soil moisture should be lower at higher temperatures because of increases in evaporation from the pots and higher rates of water loss from transpiration. [56] find the photosynthesis of *B. Allegheniensis* increases with decreases in soil moisture. These results indicate that it is critically important to consider the growth and measurement conditions when quoting or using published values of photosynthesis and other physiological parameters in the literature.

[CO_2] and nitrogen supply interactively affected J_{max} but not V_{cmax}. Elevated [CO_2] increased both photosynthetic rate and V_{cmax} and the increases were not influenced by nitrogen supply. As discussed previously, the lack of interaction between [CO_2] and nitrogen levels was related to the primary response mechanism of yellow birch to nitrogen supply. However, the direction of J_{max} response to nitrogen supply was opposite under different [CO_2] treatments. These results are in contrast to the findings of [104] on black spruce where [CO_2] and nitrogen availability interactively affected V_{cmax} but not J_{max}. The different responses of V_{cmax} and J_{max} may reflect a shift in primary limitation to photosynthesis between Rubisco limitation and RuBP regeneration limitation [30]. However, similar studies in yellow birch have reported photosynthetic downregulation under elevated [CO_2] and warmer temperatures, attributing it to a significant dilution of leaf nitrogen concentration, as evidenced by a substantial increase in total leaf area [30] [31]. Photosynthetic downregulation typically occurs when growth enhancement by a specific factor results in a dilution of leaf nitrogen concentration. Increasing nitrogen supply can reduce or avoid the dilution of leaf nitrogen and photosynthetic downregulation [27] [30].

It is interesting to note that elevated [CO_2] had no effect on stomatal conductance and transpiration. In general, elevated [CO_2] leads to decreased stomatal conductance and transpiration [105]-[108]. In the context of climate change, elevated [CO_2] reduces stomatal conductance while increasing water use efficiency (WUE), which is beneficial for plant development, especially when drought conditions are also projected to worsen [109] [110]. While the reasons for the contradicting results are not entirely clear, the lack of stomatal response to elevated [CO_2] is not uncommon in the literature [111]-[114]. There are even studies reporting increased stomatal conductance (g_s) in response to elevated [CO_2] in some plant species [110]-[116]. Thus, it can be concluded that the negative effect of elevated [CO_2] on stomatal conductance is a general rather than universal response [117].

In summary, the results of this study suggest that yellow birch may increase their photosynthetic capacity, biomass production, and growth in the future when both [CO_2] will be higher, particularly on nutrient-rich sites, due to continued increases in [CO_2] emissions. Although increasing nitrogen deposition due to continued climate change may also have positive effects on tree's response to elevated [CO_2], nitrogen deposition can have significant effects on the nutrient balance in soil, potentially influencing the availability and cycling of other nutrient elements. For instance, excessive nitrogen deposition without a proportional increase in phosphorus can lead to a nitrogen-phosphorus imbalance, altering soil microbial communities and their activities and also may increase the leaching of mobile nutrients, including potassium and calcium, which eventually lead to nutrient loss from the soil, potentially impacting the nutrient balance and fertility of the soil [118]-[121]. However, the biomass allocation between aboveground and belowground organs may be altered due to the variation in soil nitrogen availability. Additionally, the results of this study further underline the importance of considering the interactive effects of [CO_2] and other environmental factors, such as soil nitrogen availability, for predicting the growth, survival and productivity of plants and plant communities under the future climate conditions.

The findings from this study highlight significant implications for forest management under future climate change scenarios. The positive response of yellow birch to elevated [CO_2] levels, particularly under sufficient nitrogen availability, suggests opportunities to optimize forest productivity through targeted nutrient management strategies. Specifically, nitrogen fertilization in nutrient-poor sites could enhance yellow birch growth, improving both timber yields and carbon sequestration potential. Furthermore, the increased growth of yellow birch under these conditions indicates its suitability for reforestation and ecological restoration projects, making it a valuable species for mitigating climate change impacts. These results align with or diverge from findings in other tree species, providing a broader context. For instance, the reduction in root biomass allocation under elevated [CO_2] mirrors patterns seen in *Betula costata* and *B. papyrifera*, yet contrasts with species such as *Larix sibirica*, where root allocation remains less affected. These variations suggest that species-specific traits and environmental interactions play a critical role in shaping biomass allocation patterns under elevated [CO_2]. Additionally, while photosynthetic downregulation is commonly observed under elevated [CO_2] and limited nitrogen availability in many tree species, such as *Pinus taeda* and *Quercus robur*, yellow birch demonstrated stable photosynthesis across nitrogen levels in this study. This stability may reflect unique resilience mechanisms in yellow birch, providing insights for selecting climate-resilient species for forest management. However, the results also underline potential challenges related to soil nutrient depletion due to increased nutrient demand under elevated [CO_2] conditions. Forest managers must implement sustainable practices, such as balanced fertilization and monitoring of nutrient cycling, to maintain soil health and ensure the long-term productivity of forest ecosystems.

Finally, the synergistic effects of elevated [CO_2] and nitrogen supply on biomass production highlight the importance of nutrient availability for maximizing forest productivity. These results align with findings from long-term FACE experiments, suggesting that forests on nutrient-rich sites are likely to benefit more under future elevated [CO_2] conditions. However, the interactive effects observed in this study underscore the need to incorporate species-specific responses and environmental variability into predictive models of forest dynamics under climate change.

We emulated the seasonal photoperiod and daily and seasonal temperature conditions of the seed sources in our experiment and the results are in general agreement with those of longer-term FACE studies in the field. Therefore, the results may be more applicable to trees growing in the field than those from controlled environment studies where the environmental conditions are held constantly through the experiment. However, our study still has limitations. First, there were only two replicates for the [CO_2] treatment (2) due to the limitation of our greenhouse infrastructure. Second, the treatments were carried out on tree seedlings. The physiological response of trees to treatments can vary with the size and developmental stage. Third, the hourly temperatures that we used were average values of the site for the past 10 years and the actual conditions in the field fluctuate from day to day and year to year. Therefore, the experiment did not capture the effects of fluctuations in temperature, precipitation, nutrients and other environmental factors in the field. Fourth, we grew the trees in pots, which limit the extension and development of roots. Therefore, the results of this study should be used with caution and interpreted in the proper context. Additionally, the relatively short duration of the experiment (four months) limits our ability to assess the sustained impacts of elevated [CO_2] and nitrogen supply on yellow birch. Longer-term studies are needed to determine whether the observed responses are consistent over time or if they change as trees mature and as soil nutrient pools are depleted or altered. Furthermore, the controlled environment conditions do not include interactions with soil microbiota, herbivory, and other biotic factors that could significantly influence tree responses in natural ecosystems. Future studies should address these limitations by incorporating longer experimental durations, conducting field-based research, and including mature trees to better understand the long-term and ecosystem-level impacts of elevated [CO_2] and nitrogen supply on yellow birch and other forest species.

Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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