Effects of nitrogen supply on the physiological and morphological responses to elevated [CO_2] in yellow birch (*Betula alleghaniensis* Britt.)

by

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THUNDER BAY, ONTARIO

August 2023

EFFECTS OF NITROGEN SUPPLY ON THE PHYSIOLOGICAL AND MORPHOLOGICAL RESPONSES TO ELEVATED [CO$_2$] IN YELLOW BIRCH (*BETULA ALLEGHANIENSIS* BRITT.)

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A Master's Thesis Submitted in Partial Fulfillment of the Requirements for the Masters of Science in Forestry Degree

Faculty of Natural Resources Management

Lakehead University

August 2023

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ABSTRACT

Ongoing climate changes can substantially impact soil nitrogen availability through its effects on other environmental conditions such as temperature, precipitation, and the frequency and intensity of extreme whether events, eventually altering the primary productivity of plants and ecosystems. Effects of environmental changes on soil nitrogen cycling and availability vary with among season and ecosystem. Nitrogen is a critical factor regulating the photosynthetic responses of plants to elevated [CO_2] as it is a main component in photosynthetic enzymes and apparatus. Thus, changes in soil nitrogen availability will likely affect the ecophysiological responses to climate change, particularly elevated [CO_2] and the effects can change with species. A good understanding of how nitrogen supply affects the physiological and morphological responses of plants to elevated [CO_2] is critical for predicting plant performance under future climate conditions. This study examined the interactive effects of elevated [CO_2] and nitrogen (N) supply on the physiological and morphological responses in yellow birch (*Betula alleghaniensis* britt.). Seedlings were exposed to two levels of [CO_2] (ambient 400 µmol mol^{-1} versus elevated 1000 µmol mol^{-1}), and five levels of N supply (25, 50, 100, 150, and 200 mg N L^{-1}) for 4 months. Seedling height, root collar diameter, specific leaf area, biomass, biomass allocation, and foliar gas exchange parameters were assessed. The seedlings under higher nitrogen levels and elevated [CO_2] had greatest height (average increase by 4.31%) and root collar diameter (average increase 18%), but smallest specific leaf area (average decrease by 24.27%). Both [CO_2] elevation and increasing nitrogen (N) supply increased the stem dry mass, leaf dry mass and total dry mass. Stem mass ratio (SMR) increased (by 13.51%) under elevated [CO_2]. In contrast, both root to shoot ratio (RSR) (by 11.39%) and root mass ratio (RMR) (by 6.57%) decreased under elevated [CO_2]. However, the low nitrogen treatment did significantly

increase the root mass ratio and root to shoot ratio. The elevated [CO_2] significantly increased rate of net photosynthesis, both V_{cmax} (by 21.22%) and J_{max} (by 21.80%) but the effect on J_{max} was statistically significant only at the two highest nitrogen (N) treatments. Yellow birch may increase their photosynthetic capacity, biomass, and growth in the future when both [CO_2] and soil nitrogen availability will be higher due to continued increases in [CO_2] emissions and associated increase in atmospheric nitrogen deposition. The biomass allocation between above ground and below ground organs may be altered due to the variation in nitrogen availability in soil. Additionally, the results of this study further underline the importance for 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.

Keywords: climate change, yellow birch (*Betula alleghaniensis* Britt.), elevated [CO_2], soil nitrogen availability, growth, biomass, photosynthesis.

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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 a continued increase in global temperatures and changes in precipitation patterns (IPCC 2022). Elevated [CO_2] at least temporarily stimulatesplantphotosynthetic activities and growth, and influence the species competitiveness in ecosystems (Franks et al., 2013, Thompson et al., 2017). The climate change can also affect other environmental conditions such as soil nitrogen availability, eventually altering the primary productivity of plants and ecosystems (Shen et al., 2016, Maxwell et al., 2022). Furthermore, the burning of fossil fuels has substantially increased atmospheric nitrogen deposition to the soil over the last century and the increase is expected to continue in the foreseeable future (Erisman et al., 2013, Delgado-Baquerizo et al., 2016, Stevens, 2019). Elevated [CO_2] generally increases photosynthesis and plant growth and the response tends to vary with plant species and site conditions, such as soil nitrogen (N) availability (Ambebe et al., 2009, Vicente et al., 2016, Liang et al., 2020, Hu et al., 2021). A good understanding of how elevated [CO_2] and other environmental factors interactively affect the ecophysiological performance of plants is crucial for properly assessing the response of plant communities and ecosystems, particularly in regions with wide variations in environmental conditions in space and time (Bradley et al., 2010, Andresen et al., 2014, Fuchslueger et al., 2019, Wild et al., 2018).

Soil nitrogen is one of most important essential elements to the functioning of plants and terrestrial ecosystems (Maxwell et al., 2022). It is a crucial factor to regulate photosynthetic responses of plants to elevated [CO_2] as it is a main component in photosynthetic enzymes and apparatus (Kant et al., 2012). Elevated [CO_2] also affects nitrogen availability in the soil by influencing plant nitrogen uptake, soil nitrogen transformations such as nitrogen mineralization

and nitrification, and the rate of soil nitrogen cycling (Mueller et al., 2013). For instance, nitrogen acquisition is increased in the plants that grow under elevated $[CO_2]$ directly (Luo et al., 2006) and by increasing the size and depth of the root system (Finzi et al., 2007, Iversen, 2010). Moreover, elevated $[CO_2]$ can enhance litter decomposition and nitrogen mineralization (Kuzyakov, 2002, Dijkstra et al., 2008, Rütting et al., 2010, Phillips et al., 2011). Plants can acquire nitrogen more easily when organic nitrogen is mineralized to inorganic nitrogen (Ashton et al., 2010). Climate change influences the rate of organic nitrogen mineralization (Burke et al., 1997, Auyeung et al., 2013, Dawes et al., 2017, Liu et al., 2017).

Photosynthesis is one of the primary physiological processes through which nitrogen supply affects plants (Jin et al., 2015, Vicente et al., 2016, Dong et al., 2017). Elevated $[CO_2]$ generally enhances photosynthesis (Harley et al. 1992, Norby et al., 2005, McCarthy et al. 2010, Franks et al., 2013), particularly C3 plants (Leakey et al., 2009, Lee et al., 2011). Many other studies have reported increases in photosynthesis by elevated $[CO_2]$ (Zhang et al., 2008, Ambebe et al., 2010). The increases in carbohydrate production under elevated $[CO_2]$ can alter carbon and nitrogen metabolisms (Thompson et al., 2017). However, photosynthetic responses to elevated $[CO_2]$ vary with other physiological and environmental variables (Ainsworth & Long, 2005). Low nitrogen supply reduces the positive effect of elevated $[CO_2]$ on photosynthesis (Ainsworth & Long, 2005, Ribeiro et al., 2021).

Elevated $[CO_2]$ increases photosynthesis because it increases the rate of carboxylation in Rubisco and suppresses Rubisco oxygenation (Drake et al., 1997, Makino & Mae, 1999). However, long-term exposure to elevated $[CO_2]$ can cause the downregulation of photosynthetic machinery as has been found in both FACE and controlled-environment experiments (Ainsworth & Long, 2005, Warren et al., 2015). Whether photosynthetic downregulation occurs and the

degree of it depend on nutrient availability (Reich et al., 2006, Bloom et al., 2010). Inadequate nitrogen supply leads to the downregulation of photosynthetic capacity under elevated [CO_2] (Warren et al., 2015, Yin et al., 2019). Nitrogen limitation constrains the CO_2 fertilization effect on plant productivity (Terrer et al., 2019). Photosynthetic downregulation has been reported for many plant species grown under the limited nitrogen availability and elevated [CO_2] (Wujeska-Klause et al., 2019, Birami et al., 2020, Ainsworth & Long, 2021). Photosynthetic downregulation optimizes the allocation of nitrogen among different uses and organs of the plant to enhance the nitrogen use efficiency at the whole plant level in terms of growth and fitness (Deans et al., 2020). The optimization of nitrogen distribution is considered as the biochemical basis of photosynthetic downregulation (Yin et al., 2019). The dilution of tissue nitrogen also occurs due to the accumulation of excessive carbohydrates under elevated [CO_2] which reduce the mass based leaf nitrogen concentration (Rogers & Ellsworth, 2002, Kitaoka et al., 2016). The accumulation of nonstructural carbohydrates can lead to feedback inhibition to photosynthesis and subsequent downregulation (Lambers & Oliveira, 2019) and the excessive accumulation of nonstructural carbohydrates suppresses the expression of genes for Rubisco synthesis (Ghildiyal & Sharma-Natu, 2000, Kelly et al., 2013). The accumulation of nonstructural carbohydrates occurs under elevated [CO_2] and low nitrogen availability (Sugiura et al., 2017, Zheng et al., 2019). However, some studies have found no correlation between photosynthetic downregulation and leaf nitrogen concentration or nitrogen supply (Pastore et al., 2019, Silva-Pérez et al., 2020). Other studies have found that plants increase nitrogen allocation to roots at the expense of above ground organs under elevated [CO_2] (Cotrufo et al., 1998, Norby et al., 2010, Tobita et al., 2011, Xu et al., 2013). 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 plant species and plant communities under future climate conditions (Tcherkez et al., 2017). Moreover, elevated [CO_2] can inhibit nitrate assimilation in leaf tissues which in turn will increase the nutrient demand of plants (Singh et al., 2014, Li et al., 2015, Hao et al., 2016) and may result in the eventual depletion of nutrient pool in the soil (Singh et al., 2014).

Elevated [CO_2] and high nitrogen supply can have synergistic effects on the yield, and total biomass of plants (Dong et al., 2018). The synergistic effects result from the increase in photosynthetic nitrogen use efficiency under elevated [CO_2]. Increases in [CO_2] increases Rubisco carboxylation in C3 plants because CO_2 a substrate for photosynthesis and the photosynthesis of C3 plants operates under unsaturated [CO_2] (Lemonnier & Ainsworth, 2018). However, soil nitrogen limitation almost always limits the scope of plant growth enhancement by elevated [CO_2] (Kimball & Mauney, 1993, Poorter et al., 1997, Cotrufo et al., 1998, Ainsworth & Long, 2005, Feng et al., 2015).

Yellow birch (*Betula alleghaniensis* Britt.) is a deciduous tree species in the north temperate zone and has a medium growth rate (Delagrange et al., 2004). Yellow birch has great ecological and commercial value, such as quality wood products, pharmaceutical substances, etc. (Lavoie & Stevanovic, 2005). The leaf, root, stem biomass, and root biomass ratio in yellow birch have been increased under elevated [CO_2] conditions (Song & Cheng, 2010). Also, yellow birch growth is enhanced under elevated [CO_2] conditions in mesic sites (Catovsky & Bazzaz, 1999). However, yellow birch trees are more sensitive to environmental changes driven by climate change, and their mortality rate is also high under drought and freeze thaw conditions (Song & Cheng, 2010, Pike & Kern, 2022). Many other studies have reported synergistic effects of elevated concentrations of nitrogen (N) and [CO_2] on photosynthesis and biomass in other birch species (Pettersson et al., 1993, Cao et al., 2008, Esmeijer-Liu et al., 2009, Zhang & Dang,

2013). Individual and interactive effects of multiple environmental factors such as elevated [CO_2], light intensity, temperature on growth and physiology of various birch species have been studied so far (Esmeijer-Liu et al., 2009, Song & Cheng, 2010, Wang et al., 2023). Soil nitrogen is an essential macronutrient for plant function and climate change will further alter soil nitrogen availability in the future. It is, therefore, vital to understand how soil nitrogen availability will affect the responses tree physiology and growth to elevated [CO_2] and how elevated [CO_2] will affect trees growing on sites with different soil nitrogen availability. However, such knowledge on yellow birch is lacking. The objective of this study was to investigate the interactive effects of these two factors on growth and physiology of yellow birch seedlings. I hypothesized that higher nitrogen supply would enhance the magnitude of the positive effects of elevated [CO_2] on the morphological and physiological performance of yellow birch and that trees grown under lower nitrogen supply would have a higher relative response to elevated [CO_2] because elevated [CO_2] would increase nitrogen use efficiency and thus reduce the degree of nitrogen stress.

MATERIALS AND METHODS

PLANT MATERIAL AND EXPERIMENTAL DESIGN

The experiment was conducted in the Lakehead University Forest Ecology Complex in Thunder Bay. Yellow birch seeds (*Betula alleghaniensis* Britt.) were obtained from the National Tree Seed Center Fredericton, New Brunswick, Canada (seed origin: 47.45ºN, -67.45 ºW). Seeds were stratified at 4 ºC 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 photoperiod, respectively. Seedlings with relatively uniform size (2 cm average height) were transplanted into pots (14 cm height × 13 cm length × 13 cm width) filled with peat moss and vermiculite (2:1, v/v) after ten days from germination.

The treatment was comprised of two $[CO_2]$ treatments (ambient 400 µmol mol^{-1} versus elevated 1000 µmol mol^{-1}) and five nitrogen levels (25, 50, 100, 150, and 200 mg N L^{-1}). The phosphorus and potassium concentrations were 60 and 150 mg L^{-1}, respectively, for all the nitrogen treatments. The seedlings were fertilized once a week. The experiment was a split-plot design where the $[CO_2]$ treatments were applied to main plots (greenhouses), and nitrogen treatments were applied to subplots (location randomized within the greenhouse). Each $[CO_2]$ treatment was applied independently to two of the four greenhouses (two replications per treatment), whereas all the nitrogen treatments were applied to randomly located blocks within each greenhouse. The physical dimensions, layout, and environmental sensors and controllers are identical among the four greenhouses. There were ten seedlings in each treatment combination (2 levels of $[CO_2]$ and 5 levels of nitrogen concentrations), and 2 replications, 10×2×5×2=200 seedlings. The locations of the seedlings were randomized within each greenhouse. The 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 were changed with

time to emulate the natural growing season. 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). Natural light was supplemented with artificial light from high-pressure sodium lamps. When the natural day length in the greenhouse was less than needed, high-pressure sodium lamps were employed to extend the natural photoperiod. The volumetric moisture content of the growing medium was maintained 40-50% as measured with a HH2 Moisture Meter (Delta-T Devices, Cambridge, UK). The experiment lasted for 120 days. The experiment was carried out for one growing cycle between December 1, 2022, and March 31, 2023, and the environmental conditions were set to emulate the natural environmental conditions of June 4 to September 30. This study investigated the physiological and morphological responses of yellow birch seedlings to elevated [CO_2] under five different nitrogen (N) levels. The highest and the lowest nitrogen (N) concentrations in this study were little bit higher and lower respectively than that found for the yellow birch seedlings grown under controlled environments (Zhu et al., 2001, Gastaldello et al., 2007, Wang et al., 2023). Seedlings have been used in this study as evaluating the performance of seedlings is a good indicator of tree responses (Anderson-Teixeira et al., 2013). Also, the younger plants are more responsive to the increased [CO_2] (Dong et al., 2017). Thus, the consistency in results from different studies, both field research and controlled environment research by other researchers suggests that usage of seedlings under a controlled environment is suitable for examining the mechanisms of responses to multiple factors as several environmental factors can be controlled simultaneously can be a powerful tool for examining the responses of trees to the future challenging climate conditions, and (or) new locations.

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 (February 1-14). Three seedlings from each treatment combination were randomly selected for the measurements. A healthy and fully expanded leaf (2nd mature leaf out of mature leaves from the top) was measured under the following conditions: 22 °C air temperature, 50% relative humidity, 800 $\mu mol\ m^{-2}\ s^{-1}$ photosynthetically active radiation and sequentially at 400, 40, 20, 40, 60, 80, 100, 150, 200, 300, 400, 500, 700, 1000, 1100, 1400 and 1600 $\mu mol\ mol^{-1}\ CO_2$ for the ambient $[CO_2]$ measurement and sequentially at 1000, 40, 20, 40, 60, 80, 100, 150, 200, 300, 400, 500, 700, 1000, 1100, 1400 and 1600 $\mu\ mol\ mol^{-1}\ CO_2$ for the elevated $[CO_2]$ measurements. The measurements were carried out between 7:00 a.m. and 3:00 p.m. when our tests showed relatively stable gas exchange measurements (after 3-4 minutes in each leaf). The net photosynthetic rate at growth $[CO_2]$ (P_n) and the corresponding stomatal conductance (g_s), transpiration rate (E), and instantaneous water-use efficiency (iWUE) were extracted from the above measurements for statistical analyses. The sequence of measurements among different treatments were randomized to avoid systematic errors.

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 WinFolia 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 stem were measured separately on an electronic balance. The dry mass of the leaves for the specific leaf area measurement were 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 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/total leaf and stem dry mass).

A/CI CURVE FITTING

A biochemical model of photosynthesis was used to derive photosynthetic parameters from each set of gas exchange measurements (Farquhar & von Caemmerer, 1982). The parameters estimated were the maximum rate of Rubisco carboxylation (V_{cmax}) and the maximum rate of electron transport for RuBP regeneration under saturating light (J_{max}). The model was fit employing a "default" fitting method using the "fitaci" function of the "plantecophys" package (Duursma., 2015) on the R software package 4.2.2 (R Development Core Team 2023).

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) using the R software (Version 4.2.2, R Development Core Team 2023) 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 $P \leq 0.05$. When ANOVA showed a significant ($P \leq 0.05$) 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 causes to increase 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 the R studio software (Version 4.2.2, R Development Core Team 2023).

<p style="text-align:center">RESULTS</p>

GROWTH

[CO_2] and nitrogen supply had 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] (Fig. 1a). Elevated [CO_2] significantly increased seedling height

growth only under the 150 mg N L^{-1} nitrogen treatment (average increase by 4.31%) (Figure 1a).

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 1b). Seedling RCD generally increased with increasing nitrogen supply in both ambient

and elevated [CO_2] but the increases were generally greater under the elevated than ambient

[CO_2] (by 18.12%), particularly at higher nitrogen levels (Figure 1b).

Table 1. Summary of ANOVA (*P*-value, F value and Degree of freedom (DF)) results for height,
RCD, and specific leaf area (SLA) of yellow birch seedlings grown under two [CO_2] (C) (400

Vs. 1000 µmol mol^{-1}) and five levels of nitrogen (N) supply. The numbers in bold font are statistically significant ($P \leq 0.05$).

Variable	C (DF = 1)	N (DF = 4)	C × N (DF = 4)
Height			
F	2.248	127.492	3.474
P	0.137	**<0.001**	**0.011**
Root collar diameter			
F	75.105	108.650	5.817
P	**<0.001**	**<0.001**	**<0.001**
Specific leaf area			
F	150.875	14.426	3.708
P	**<0.001**	**<0.001**	**0.0076**
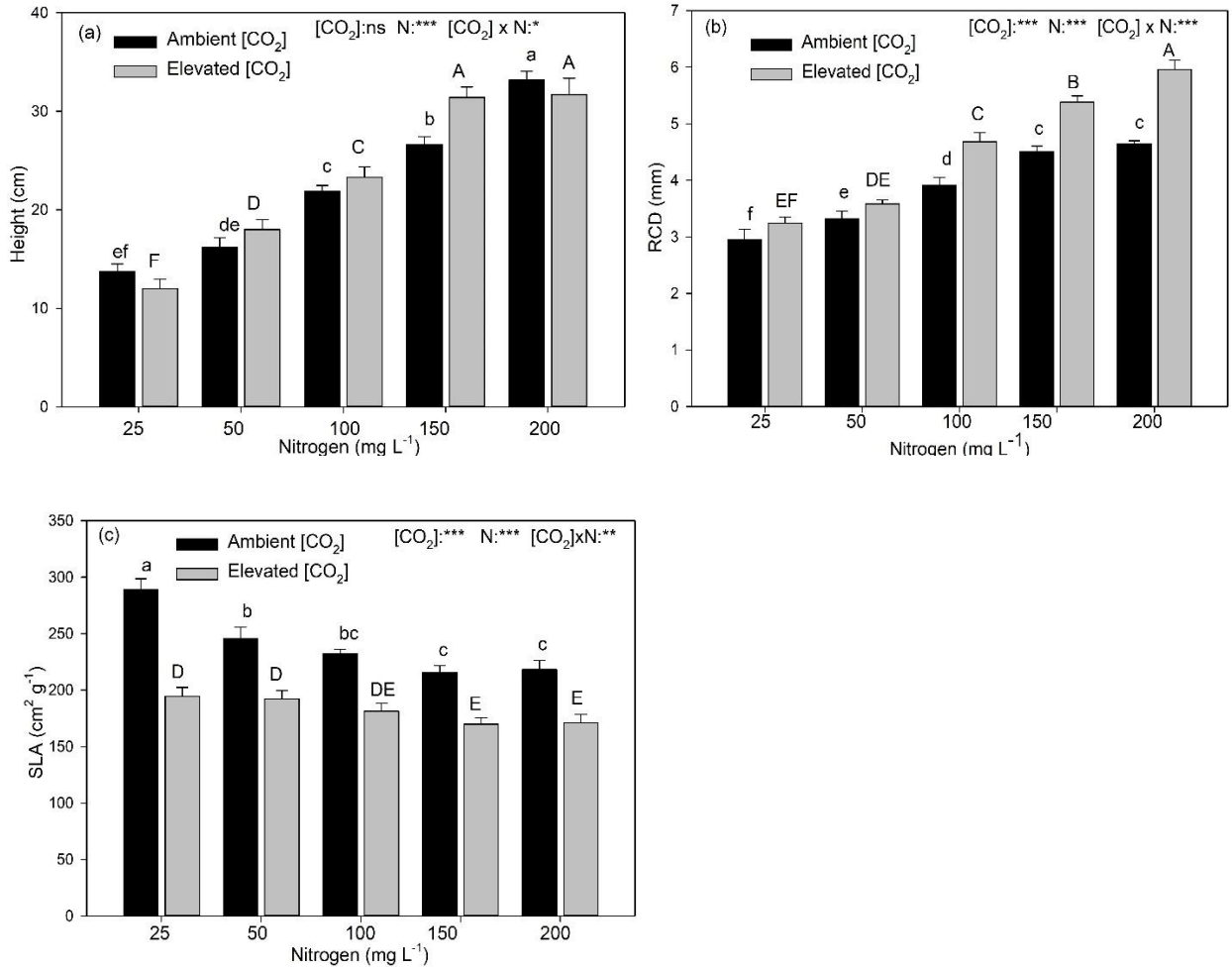
Figure 1: Mean (+SE), (a) height growth, (b) RCD, (c) specific leaf area (SLA) (n=5) of yellow birch seedlings grown under two levels of [CO_2] (ambient Vs elevated), five levels of nitrogen supply for 4 months. Data are pooled across [CO_2] for (c) left (n =20): five seedlings with two replications per treatment, two levels of [CO_2], 5 x 2 x2=20). 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.

The specific leaf area (SLA) generally declined with increases in nitrogen supply but not all the

differences between two adjacent levels of nitrogen supply were statistically significant (Figure

1d). The elevated [CO$_2$] treatment significantly reduced SLA across all nitrogen treatments

(average by 24.27%) (Figure 1d).

BIOMASS AND BIOMASS ALLOCATION

Root, stem, leaf and total biomass all increased with increasing nitrogen supply, but not all the

differences between adjacent nitrogen levels were statistically significant (between two lowest

nitrogen levels and between two highest nitrogen levels) (Figure 2). The elevated [CO$_2$]

significantly increased total seedling biomass (relative increase of 15.95%), stem biomass

(relative increase of 31.36%), leaf biomass (relative increase of 19.89%), and root biomass

(relative increase of 6.11%), but the effect on root biomass was not statistically significant

(Figure 2, Table 2).

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 grown under two [CO$_2$] (C) (400 Vs. 1000 μmol mol^{-1}) and five levels of nitrogen (N) supply. The numbers in bold font are statistically significant ($P \leq 0.05$).

Variable	C (DF = 1)	N (DF = 4)	C × N (DF = 4)
Root DM			
F	0.983	38.401	0.030
P	0.324	**<0.001**	0.998
Leaf DM			
F	12.663	82.495	0.226
P	**<0.001**	**<0.001**	0.922971
Stem DM			
F	19.135	52.168	1.346
P	**<0.001**	**<0.001**	0.259
Total DM			
F	9.150	69.304	0.237
P	**<0.001**	**<0.001**	0.91666

Figure 2: Mean (+SE), biomass of yellow birch seedlings grown under two levels of $[CO_2]$ (ambient Vs elevated), five levels of nitrogen supply for 4 months. Data are pooled across $[CO_2]$ for (a), (b), (c), (d) left (n =20): five seedlings with two replications per treatment, two levels of $[CO_2]$, 5 x 2 x2=20). 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 3. Summary of ANOVA (P-value, F value and Degree of freedom (DF)) results for leaf mass ratio (LMR), stem mass ratio (SMR), root mass ratio (RMR), root to shoot ratio (RSR) of yellow birch seedlings grown under two [CO_2] (C) (400 Vs. 1000 µmol mol^{-1}) and five levels of nitrogen (N) supply. The numbers in bold font are statistically significant ($P \leq 0.05$).

Variable	C (DF = 1)	N (DF = 4)	C × N (DF = 4)
LMR			
F	0.156	3.863	0.075
P	0.69373	**<0.001**	0.98971
SMR			
F	16.141	1.860	0.393
P	**<0.001**	0.124356	0.812843
RMR			
F	5.638	4.045	0.333
P	**0.01970**	**0.00462**	0.85491
RSR			
F	5.661	4.916	0.207
P	**0.01946**	**0.00125**	0.93385

Figure 3: Mean (+SE) biomass allocation of yellow birch seedlings grown under two levels of [CO_2] (ambient Vs elevated), five levels of nitrogen supply for 4 months. Data are pooled across [CO_2] for (a), (b), (c), (d) left (n =20): five seedlings with two replications per treatment, two levels of [CO_2], 5 x 2 x2=20). 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.

Root to shoot ratio (RSR) (0.955) and root mass ratio (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 3a,3c). In contrast, the leaf mass ratio

was significantly smaller in the lowest nitrogen treatment (0.322) than other nitrogen levels

(Figure 3b). The elevated [CO_2] significantly decreased RSR (by 11.39%) and RMR (by 6.57%),

but significantly increased SMR (by 13.51%) (Figure 3a,3c,3d).

FOLIAR GAS EXCHANGE

Elevated [CO_2] treatment significantly increased the rate of net photosynthesis (P_n) (elevated:

9.43 μ mol m^{-2} s^{-1}, ambient: 4.65 μ mol m^{-2} s^{-1}) and instantaneous water use efficiency measured

at the growth CO_2 (iWUE) (by 65.71%) (Figure 4a, Figure 4b, Table 4). Neither [CO_2] nor

nitrogen supply significantly affected stomatal conductance and transpiration rate (Table 4).

Table 4. Summary of ANOVA (*P*-value, F value and Degree of freedom (DF)) results for rate of net photosynthesis (P$_n$), stomatal conductance (g$_s$), transpiration rate (E), instantaneous water use efficiency (iWUE), maximum rate of Rubisco carboxylation (*V$_{cmax}$*), maximum of photosynthetic electron transport rate (*J$_{max}$*) of yellow birch seedlings grown under two [CO$_2$] (C) (400 Vs. 1000 µmol mol^{-1}) and five levels of nitrogen (N) supply. The numbers in bold font are statistically significant ($P \leq 0.05$).

Variable	C (DF = 1)	N (DF = 4)	C × N (DF = 4)
P$_n$			
F	161.581	0.476	1.374
P	**<0.001**	0.753	0.256
g$_s$			
F	0.934	1.201	0.816
P	0.338	0.322	0.521
E			
F	3.622	0.935	0.226
P	0.0628	0.4512	0.9224
WUE			
F	35.281	1.736	0.421
P	**<0.001**	0.157	0.792
Vcmax			
F	11.713	2.548	0.696
P	**0.00125**	0.05065	0.59849
Jmax			
F	26.043	0.931	2.607
P	**<0.001**	0.4536	**0.0466**
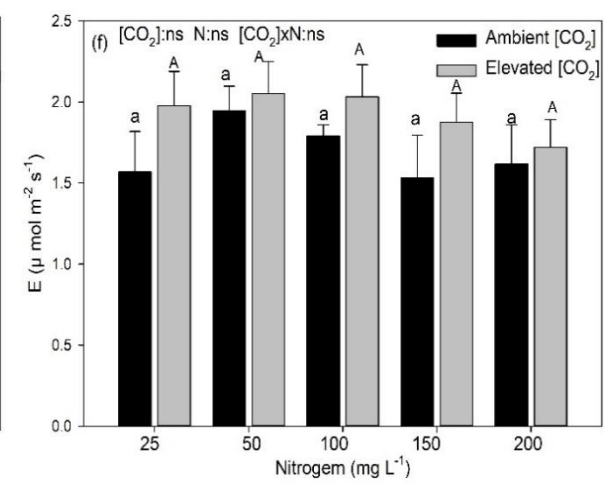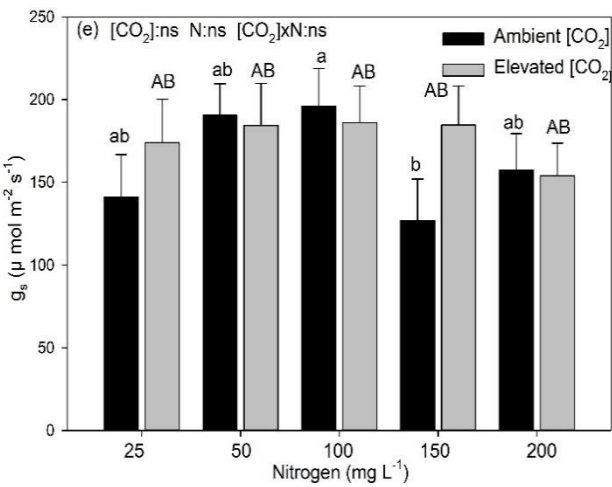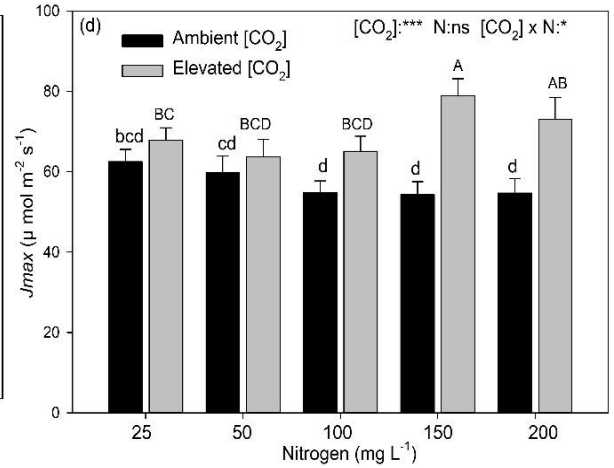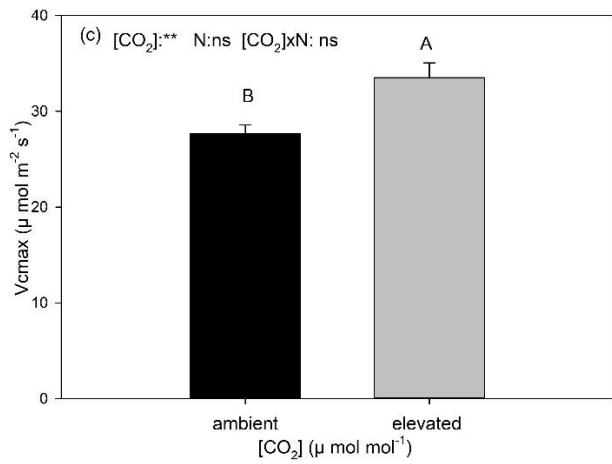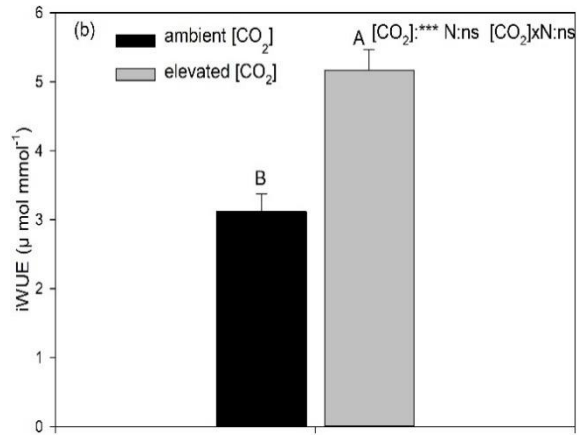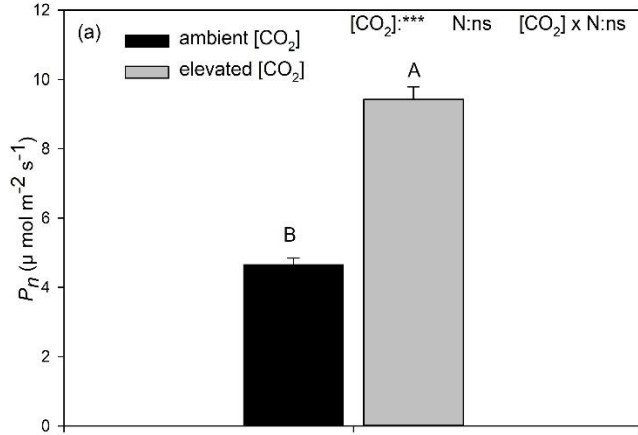
Figure 4: Mean (+SE) (a) rate of net photosynthesis (P_n), (b) instantaneous water use efficiency (iWUE), (c) photosynthetic carboxylation rate (V_{cmax}), (d) photosynthetic electron tr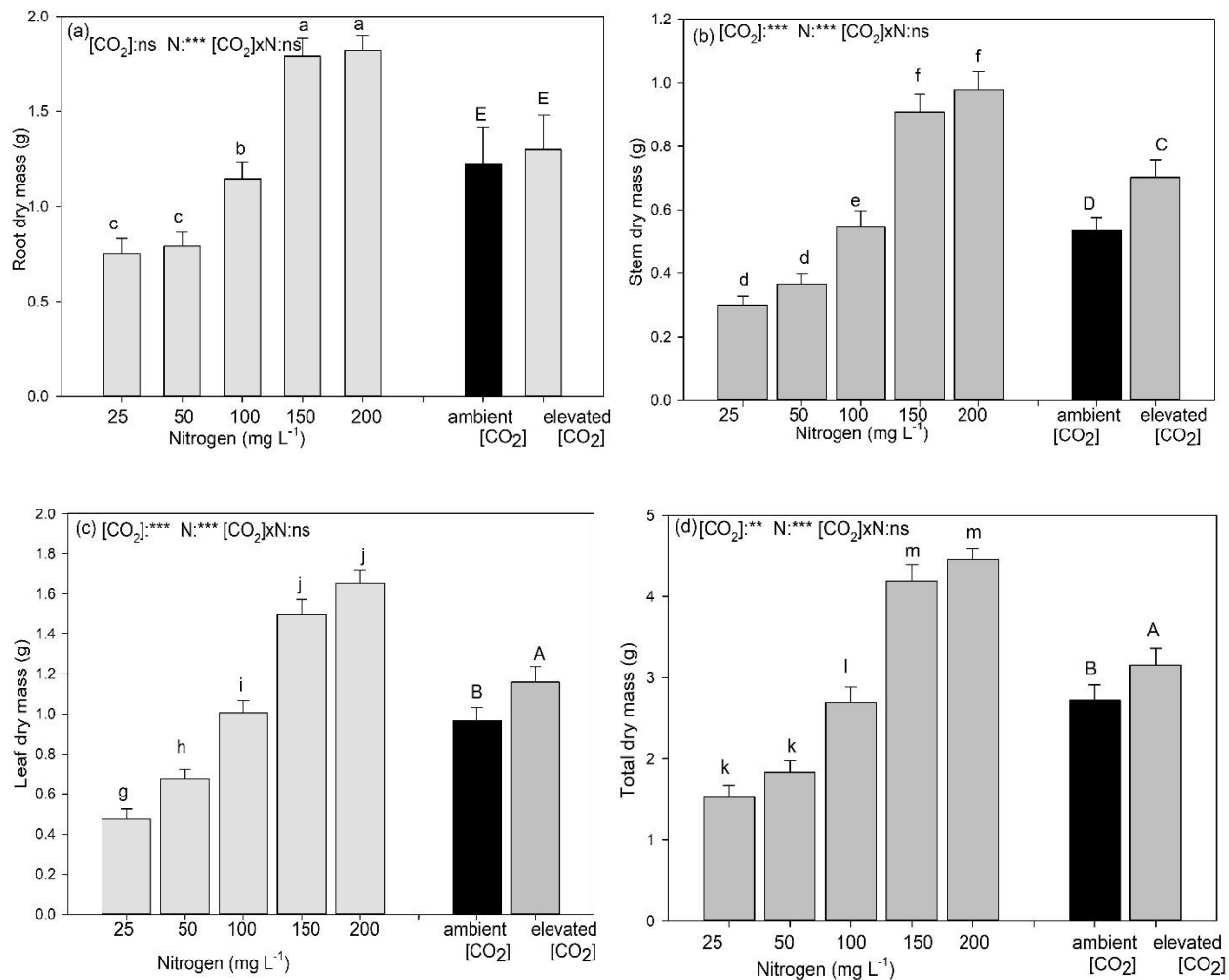ansport rate (J_{max}), (e) stomatal conductance (g_s), (f) transpiration rat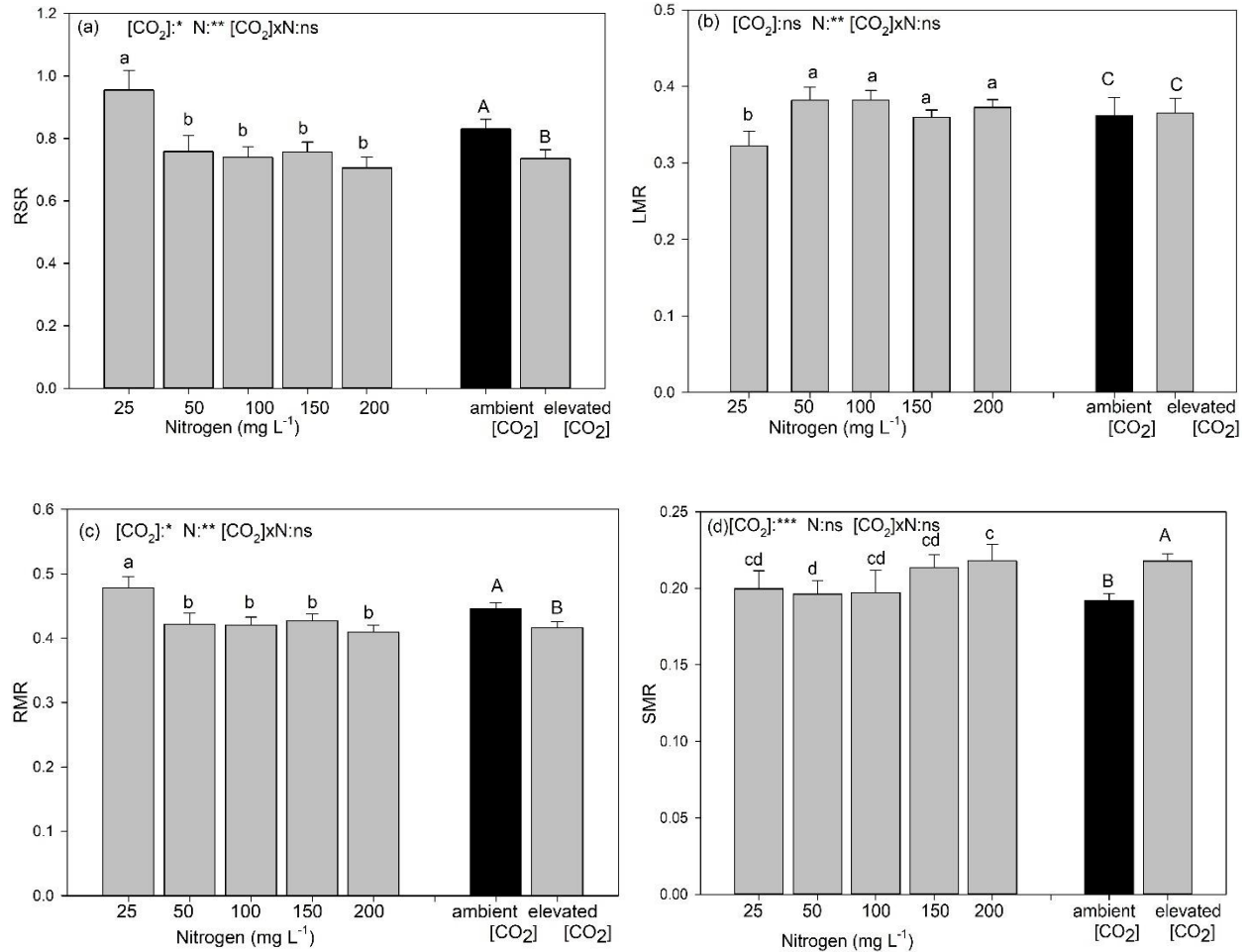e (E) of yellow birch seedlings grown under two levels of [CO_2] (ambient Vs elevated), five levels of nitrogen supply for 4 months. Data are pooled across [CO_2] for (a), (b), (c) (n =12): three seedlings with two replications per treatment, two levels of [CO_2], 3 x 2 x2=12). Means with different letters 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.

The elevated [CO_2] significantly increased both the maximum rate of Rubisco carboxylation (by 21.22%) (V_{cmax}, Figure 4c) and the maximum photosynthetic electron transport rate J_{max} (by 21.80%) (Figure 4d). J_{max} was significantly higher in the two highest nitrogen treatments than other nitrogen levels in seedlings grown under the elevated [CO_2] (150 mg L^{-1}: 78.88 μ mol m^{-2} s^{-1}, 200 mg L^{-1}: 73.07 μ mol m^{-2} s^{-1}), but nitrogen treatment had no significant effect on J_{max} in the ambient [CO_2] treatment (Figure 4d).

DISCUSSION

The elevated [CO_2] increased seedling height and root collar diameter growth and the increases were greater at higher nitrogen (N) levels. However, this synergistic effect on height growth only occurred at 150 mg N L^{-1} nitrogen supply. The results are in general agreement with Cao et al., (2008) on white birch (*Betula papyrifera* Marsh.). This can be explained as greater stimulation of aboveground growth by elevated [CO_2] under higher nitrogen supply due to increasing nitrogen use efficiency for photosynthesis and plant growth (Radoglou et al., 1992, Zerihun, 2000, Mohamed et al., 2013). The lack of significant positive effect of elevated [CO_2] on height growth has been observed in several other tree species such as *Eucalyptus miniata* (Duff et al., 1994) and *Populas* (Liberloo et al., 2005). Generally, elevated [CO_2] increased the height growth of plant species (Cao et al., 2008, Lamichaney et al., 2021). Plant height is vital morphological trait that directly related to plant growth (Wang et al., 2018). Height growth is one of the vital determinant factor for the survival of plant species and used as an indicator of fitness (Ying & Yanchuk, 2006). Adequate height growth in early stages is important for the establishment of yellow birch, particularly regeneration in hardwood stands (Wang, 1965).

Growth is generally positively correlated with specific leaf area (SLA) (Poorter et al., 1990, Cornelissen et al., 1996, Atkin et al., 1998, Reich et al., 1998, Lambers & Poorter, 2004, Shipley, 2006). 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 (Cao et al., 2008), barley and tomato plants (Chen et al., 2022). The reduction in specific leaf area (SLA) caused by elevated [CO_2] can be interpreted as evidence for the accumulation of carbohydrates in the leaf and the subsequent dilution of nutrients (Roumet et al., 1999, Zhang et al., 2006). These results suggest that yellow birch may have faster growth

resulting with thicker leaves due to the increased carbohydrate production under future $[CO_2]$ conditions in nitrogen rich sites in soil.

Both $[CO_2]$ elevation and increasing nitrogen (N) supply increased the stem dry mass, leaf dry mass and total dry mass. These results are consistent with the findings of several studies (Catovsky & Bazzaz, 1999, Dijkstra et al., 2002, Cao et al., 2008b, Song & Cheng, 2010, Arsić et al., 2021). The $[CO_2]$ effect may be caused by the fertilization effect of elevated $[CO_2]$ on plant growth and biomass enhancement (Reich et al., 2014). Increased photosynthesis under elevated $[CO_2]$ lead to enhance the carbohydrate production which serves as building blocks for plant biomass production (Körner, 2006). Increasing biomass under higher nitrogen (N) supply also has been reported by several studies (Nguyen et al., 2003, Boussadia et al., 2010, Chen et al., 2018). This may be caused due to nitrogen is a critical factor regulating the photosynthetic responses of plants to elevated $[CO_2]$ as it is a main component in photosynthetic enzymes and structures (Kant et al., 2012). Photosynthetic enhancement under higher nitrogen supply may explained as increase in chlorophyll content and Rubisco activity (Evans & Terashima, 1987, Fredeen et al., 1991, Fahl et al., 1994, Verhoeven et al., 1997, Tóth et al., 2002) because up to 75% leaf nitrogen contained in chloroplasts, especially invested in Rubisco (Brown, 1978), consequently increasing the biomass production. Elevated $[CO_2]$ enhance the root biomass and growth by making larger/deeper root system and enhanced whole plant nitrogen sink strength (Finzi et al., 2007, Iversen, 2010). However, the elevated $[CO_2]$ alone did not have a significant effect on root dry mass in this study. While the reason for this result can't be entirely explained, but similar effect has been reported by Benlloch-Gonzalez et al., (2014) on wheat that root biomass enhancing effect by elevated $[CO_2]$ was constrained by high temperature. These contrasting responses of belowground biomass and growth to elevated $[CO_2]$ appear to be related

to plant genotypic differences (Benlloch-Gonzalez et al., 2014). Therefore, the yellow birch biomass may be enhanced under future [CO_2] levels along with soil nitrogen rich sites which may lead to enhance plant productivity and yield.

Stem mass ratio (SMR) increased under elevated [CO_2]. Similar results can be found in some other studies (Butterly et al., 2015, Morita et al., 2016) . For instance, Morita et al. (2016) found that stem mass ratio (SMR) is increased under elevated [CO_2], which was in line with elevated [CO_2] promotes stem growth. Zhang & Dang, (2006) reported that high nutrient supply decreased root mass ratio (RMR) under elevated [CO_2] in white birch (*Betula papyrifera* Mash.). Yazaki et al. (2001) observed elevated [CO_2]-induced stimulation of stem diameter growth of *Larix sibirica* under relatively high nutrient conditions. This can be explained as increased biomass density of the stem under elevated [CO_2] (Zhang et al., 2006). In contrast, both root to shoot ratio (RSR) and root mass ratio (RMR) decreased under elevated [CO_2]. Tobita et al., (2019) has reported that biomass allocation to roots decreased with elevated [CO_2] in *Fagus crenata,* broad leaf tree species. However, the low nitrogen treatment did significantly increase the root mass ratio and root to shoot ratio, supporting the theory that low nutrient supply stimulates biomass allocation to roots (Walker and Gessel, 1990, Marschner, 1995, Larcher, 2003). Generally, plants grow under elevated [CO_2] exhibit greater leaf thickness, more leaves per plant (Pritchard et al., 1999). Interestingly, elevated [CO_2] had no effect on the leaf mass ratio (LMR) of yellow birch in this study. While this result is inconsistent with the majority of the literature, some other studies have reported that the elevated [CO_2] had little or no impact on leaf initiation in plants which may indirectly affect for reducing the leaf biomass (Ford and Thorne, 1967, Rogers et al., 1980, Jones et al., 1984). So, it is suggested that the effect of elevated [CO_2] on leaf development may depend on other environmental factors or plant

developmental stage (Ackerly et al., 1992). Also, these findings support other researchers' findings that [CO_2] has no effect on biomass allocation among roots and shoots (Bosaca et al., 1995, Gebauer et al., 1996, Tingey et al., 1996, Tissue et al., 1997, Curtis & Wang, 1998). Long term FACE studies suggest that elevated [CO_2] has greater positive effects on the growth of aboveground than belowground parts of plants under higher nitrogen supply (De Graaff et al., 2006). Plants adjust the balance between source and sink by altering the biomass allocation among different organs to maximize the total carbon gain (Piñero et al., 2016, Wang et al., 2022). The greater stimulation of aboveground growth by elevated [CO_2] under higher nitrogen supply may be attributed to increases in nitrogen use efficiency for photosynthesis and plant growth as reported in the literature (Radoglou et al., 1992, Zerihun, 2000, Mohamed et al., 2013).

The hypothesis that on the enhancing effect of higher nitrogen (N) on the positive effect of elevated [CO_2] on physiological performance was partially supported: The elevated [CO_2] significantly increased both V_{cmax} and J_{max} but the effect on J_{max} was statistically significant only at the two highest nitrogen (N) treatments. Similar findings have been reported about the enhancing effect of higher nitrogen supply on photosynthesis under elevated [CO_2] (Ceulemans et al., 1997, Curtis et al., 2000, Zhang & Dang, 2006, Zhang et al., 2013). Photosynthetic enhancement under elevated [CO_2] can be explained as increasing the rate of carboxylation in Rubisco while decreasing the rate of oxygenation (Drake et al., 1997, Makino & Mae, 1999) whereas photosynthetic enhancement under higher nitrogen supply may explained as increase in chlorophyll content and Rubisco activity (Evans & Terashima, 1987, Fredeen et al., 1991, Fahl et al., 1994, Verhoeven et al., 1997, Tóth et al., 2002) because up to 75% leaf nitrogen contained in chloroplasts, especially invested in Rubisco (Brown, 1978). V_{cmax} represents the maximum [CO_2] assimilation capacity of the primary photosynthetic enzyme Rubisco and J_{max} reflect the

maximum capacity of the electron transport chain for photosynthesis (Lambers & Oliveira, 2019). Tedla et al., (2021) has reported that increased photosynthetic capacity (particularly J_{max}) under elevated [CO_2] condition in white birch (*Betula papyrifera* Marsh). But, Dang et al., (2021) has reported that elevated [CO_2] and nitrogen availability interactively affected for the photosynthetic capacity via interactive effect on V_{cmax}, but not J_{max} in black spruce seedlings *Picea mariana* [Mill.] which is contradict to my observation. So, plants have various strategies to maintain J_{max} to V_{cmax} coordination that prevent from photoinhibition when carboxylation is limiting to maximize photosynthetic rates when light is limiting (Walker et al., 2014). This study suggests that stimulation of photosynthetic carbohydrate production in yellow birch by elevated [CO_2] can be enhanced by increasing nitrogen supply through fertilization, improved nutrient cycling. Therefore, yellow birch may have higher photosynthesis under future [CO_2] conditions with higher nitrogen availability in soil as climate change will further alter soil nitrogen availability in soil and further increasing atmospheric nitrogen deposition to the soil due to burning fossil fuels. However, the long-term exposure to elevated [CO_2] cause to the downregulation of photosynthesis which has been observed under both FACE studies and chamber experiments (Ainsworth & Long, 2005, Warren et al., 2015).

It is interesting to note that elevated [CO_2] had no effect on stomatal conductance and transpiration which is contradict to the general findings. Elevated [CO_2] generally enhance the photosynthesis and consequently plant growth and production (Ainsworth & Rogers, 2007, Xu et al., 2013). Elevated [CO_2] decrease the stomatal conductance but promote water use efficiency (WUE) which benefit for plant growth, especially within climate change context drought conditions are expected to rise (Leakey et al., 2009, Sreeharsha et al., 2015). Sreeharsha et al., (2015) reported that elevated [CO_2] increased the instantaneous iWUE due to simultaneously

maintaining both higher photosynthesis and stomatal conductance (g_s). While the reasons for this result cannot be entirely explained, several studies have reported the several different stomatal responses to elevated [CO_2]. Elevated [CO_2] generally cause to decrease the stomatal conductance and leaf transpiration (Ainsworth & Rogers, 2007, Teng et al., 2009, Katul et al., 2010, Gao et al., 2015). However, few experiments have reported that stomatal conductance (g_s) did not respond to [CO_2] concentrations in an obvious way (Ellsworth et al., 2012, Haworth et al., 2013, Ward et al., 2013, Bernacchi & VanLoocke, 2015, DaMatta et al., 2016). In contrast, stomatal conductance (g_s) increase has been observed under elevated [CO_2] in some plant species (Uddling et al., 2009, Zinta et al., 2014, Sreeharsha et al., 2015). Thus, stomatal responses under elevated [CO_2] depend on many factors (Xu et al., 2016). For instance, stomatal behavior may be altered by several environmental factors alone or in combination such as water status, temperature, light (Lee et al., 2008, Perez-Martin et al., 2009, Hubbart et al., 2013, Laanemets et al., 2013, Igut et al., 2015). Also, stomatal short term behavior and long term developmental responses to environmental changes might occur together depending on plant species and genotypes (Gray et al., 2000, Ainsworth & Rogers, 2007, Haworth et al., 2013, DaMatta et al., 2016). Thus, it can be concluded that elevated [CO_2] effect on decreasing stomatal conductance is a general rather than universal response because of some unexpected factor effects (Xu et al., 2016). Therefore, yellow birch may have higher photosynthesis under future [CO_2] conditions with higher nitrogen availability in soil.

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] and soil nitrogen availability will be higher due to continued increases in [CO_2] emissions and associated increase in atmospheric nitrogen deposition. However, the biomass allocation between aboveground and

belowground organs may be altered due to the variation in nitrogen availability in soil.

Additionally, the results of this study further underline the importance for 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.

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APPENDIX

Table 5. Growth characteristics (height, RCD, SLA) of yellow birch seedlings grown under two CO_2 (400 vs. 1000 µmol mol^{-1}) and five levels of N supply (25, 50, 100, 150, and 200 mg N L^{-1}).

CO_2	N	Height (cm)	RCD (mm)	SLA (cm^2 g^{-1})
ambient	25	13.72 ± 0.77 ef	2.95 ± 0.19 f	289.03 ± 9.48 a
	50	16.21 ± 0.98 de	3.32 ± 0.14 e	245.59 ± 10.08 b
	100	21.88 ± 0.59 c	3.92 ± 0.13 d	232.16 ± 4.12 bc
	150	26.62 ± 0.78 b	4.51 ± 0.09 c	215.85 ± 6.02 c
	200	33.15 ± 0.90 a	4.65 ± 0.05 c	218.24 ± 8.14 c
elevated	25	11.99 ± 0.95 f	3.24 ± 0.11 ef	194.57 ± 7.89 d
	50	18.01 ± 0.99 d	3.59 ± 0.07 de	192.40 ± 7.16 d
	100	23.3 ± 1.08 c	4.68 ± 0.16 c	181.39 ± 7.08 de
	150	31.4 ± 1.08 a	5.39 ± 0.11 b	169.85 ± 5.63 e
	200	31.69 ± 1.67 a	5.96 ± 0.16 a	171.25 ± 7.51 e

Note: Each value represents mean ± SE (n=10). Different letters within the same column indicated statistically significant differences between treatments (Fisher's least significant difference post hoc test (p < 0.05). Variables: Height. RCD (root collar diameter), SLA (specific leaf area).

Table 6. Biomass characteristics (root, leaf, stem, total dry mass) of yellow birch seedlings grown under two CO_2 (400 vs. 1000 µmol mol^{-1}) and five levels of N supply (25, 50, 100, 150, and 200 mg N L^{-1}).

CO_2	N	Root DM (g)	Leaf DM (g)	Stem DM (g)	Total DM (g)
ambient	25	0.70 ± 0.11 d	0.42 ± 0.05 g	0.27 ± 0.04 e	1.39 ± 0.18 e
	50	0.75 ± 0.12 d	0.59 ± 0.07 ef	0.31 ± 0.05 e	1.65 ± 0.22 e
	100	1.11 ± 0.12 bc	0.94 ± 0.07 cd	0.48 ± 0.08 cd	2.53 ± 0.26 cd
	150	1.76 ± 0.14 a	1.37 ± 0.09 b	0.79 ± 0.06 b	3.91 ± 0.27 b
	200	1.81 ± 0.14 a	1.51 ± 0.08 b	0.83 ± 0.05 b	4.14 ± 0.21 ab
elevated	25	0.81 ± 0.12 cd	0.53 ± 0.08 fg	0.33 ± 0.04 de	1.66 ± 0.23 e
	50	0.83 ± 0.09 cd	0.76 ± 0.06 de	0.43 ± 0.04 de	2.01 ± 0.17 de
	100	1.19 ± 0.13 b	1.07 ± 0.10 c	0.61 ± 0.07 c	2.87 ± 0.27 c
	150	1.83 ± 0.13 a	1.63 ± 0.11 ab	1.03 ± 0.09 a	4.48 ± 0.28 ab
	200	1.84 ± 0.08 a	1.81 ± 0.07 a	1.13 ± 0.07 a	4.77 ± 0.15 a

Note: Each value represents mean ± SE (n=10). Different letters within the same column indicated statistically significant differences between treatments (Fisher's least significant difference post hoc test (p < 0.05). Variables: Root DM (root dry mass), Leaf DM (leaf dry mass), Stem DM (stem dry mass), Total DM (total dry mass).

Table 7. Biomass allocation (LMR, SMR, RMR, RSR) of yellow birch seedlings grown under two CO_2 (400 vs. 1000 µmol mol^{-1}) and five levels of N supply (25, 50, 100, 150, and 200 mg N L^{-1}).

CO_2	N	LMR	SMR	RMR	RSR
ambient	25	0.33 ± 0.03 b	0.20 ± 0.01 cd	0.48 ± 0.03 a	0.97 ± 0.11 a
	50	0.39 ± 0.03 a	0.18 ± 0.01 d	0.44 ± 0.03 abc	0.81 ± 0.08 abcd
	100	0.38 ± 0.02 a	0.18 ± 0.02 cd	0.43 ± 0.01 abc	0.78 ± 0.04 bcd
	150	0.35 ± 0.01 ab	0.20 ± 0.01 bcd	0.45 ± 0.01 ab	0.81 ± 0.03 abc
	200	0.37 ± 0.02 ab	0.20 ± 0.01 bcd	0.43 ± 0.02 abc	0.78 ± 0.05 bcd
elevated	25	0.32 ± 0.02 b	0.20 ± 0.02 bcd	0.48 ± 0.02 a	0.94 ± 0.07 ab
	50	0.38 ± 0.02 a	0.21 ± 0.01 abc	0.41 ± 0.02 bc	0.71 ± 0.07 cd
	100	0.38 ± 0.02 a	0.21 ± 0.01 abc	0.41 ± 0.02 bc	0.70 ± 0.06 cd
	150	0.37 ± 0.01 ab	0.23 ± 0.01 ab	0.41 ± 0.02 bc	0.70 ± 0.05 cd
	200	0.38 ± 0.01 a	0.23 ± 0.01 a	0.39 ± 0.01 c	0.63 ± 0.03 d

Note: Each value represents mean ± SE (n=10). Different letters within the same column indicated statistically significant differences between treatments (Fisher's least significant difference post hoc test (p < 0.05). Variables: LMR: leaf mass ratio. SMR: stem mass ratio. RMR: root mass ratio. RSR: root to shoot ratio.

Table 8. Foliar gas exchange (Pn, gs, E, iWUE, Vcmax, Jmax) of yellow birch seedlings grown under two CO2 (400 vs. 1000 µmol mol−1) and five levels of N supply (25, 50, 100, 150, and 200 mg N L-1).

CO_2	N	Pn (µ mol m^{-2} s^{-1})	gs (µ mol m^{-2} s^{-1})	E (µ mol m^{-2} s^{-1})	iWUE (µ mol mol^{-1})	Vcmax (µ mol m^{-2} s^{-1})	Jmax (µ mol m^{-2} s^{-1})
ambient	25	0.48 ± 0.48 b	141.17 ± 25.68 ab	1.57 ± 0.25 a	3.42 ± 0.77 bc	30.55 ± 2.82 abc	62.49 ± 3.11 bcd
	50	4.3 ± 0.33 b	190.5 ± 19.08 ab	1.95 ± 0.15 a	2.31 ± 0.28 c	26.09 ± 2.39 c	59.81 ± 4.08 cd
	100	5.2 ± 0.37 b	196 ± 22.93 a	1.79 ± 0.07 a	2.94 ± 0.14 bc	26.43 ± 1.65 c	54.86 ± 2.90 d
	150	4.47 ± 0.52 b	126.83 ± 25.11 b	1.53 ± 0.27 a	3.46 ± 0.61 bc	28.63 ± 1.35 bc	54.29 ± 3.25 d
	200	4.7 ± 0.44 b	157.17 ± 22.23 ab	1.62 ± 0.24 a	3.46 ± 0.82 bc	26.56 ± 2.05 c	54.67 ± 3.67 d
elevated	25	9.3 ± 0.46 a	174 ± 26.15 ab	1.98 ± 0.21 a	5.03 ± 0.64 a	36.85 ± 5.36 ab	67.79 ± 3.16 bc
	50	8.78 ± 0.27 a	184.33 ± 25.40 ab	2.05 ± 0.20 a	4.54 ± 0.57 ab	29.29± 2.58 bc	63.72 ± 4.31 bcd
	100	8.42 ± 0.65 a	186 ± 22.27 ab	2.03 ± 0.20 a	4.24 ± 0.32 ab	28.19 ± 2.13 bc	65.07 ± 3.78 bcd
	150	11.03 ± 1.26 a	184.67 ± 23.61 ab	1.88 ± 0.18 a	6.17 ± 0.82 a	38.22 ± 2.87 a	78.88 ± 4.27 a
	200	9.6 ± 0.82 a	154 ± 19.72 ab	1.72 ± 0.17 a	5.86 ± 0.73 a	35.05 ± 2.28 ab	73.07 ± 5.45 ab

Note: Each value represents mean ± SE (n=6). Different letters within the same column indicated statistically significant differences between treatments (Fisher's least significant difference post hoc test (p < 0.05). Variables: Pn (rate of net photosynthesis), gs (stomatal conductance), E (transpiration rate),

iWUE (instantaneous water-use efficiency), Vcmax (maximum rate of Rubisco carboxylation), Jmax (maximum of photosynthetic electron transport rate).