

Nutrient and [CO₂] elevation had synergistic effects on biomass production but not on biomass allocation of white birch seedlings

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Abstract

This study investigated the interactive effects of nutrient supply and [CO₂] elevation on the growth and biomass of white birch seedlings (*Betula papyrifera* Mash.). The seedlings were grown under two nutrient regimes (100 ppm N, 44 ppm P, 83 ppm K and 1/10 the strength of these levels) and two [CO₂] levels (360 and 720 ppm) for 3.5 months. The [CO₂] elevation had no significant effect on either height (*H*) or root collar diameter (RCD), but significantly reduced specific leaf area. The high nutrient treatment increased both *H* and RCD. High nutrient significantly increased total, stem and leaf biomass under both [CO₂] treatments but the effect was greater under elevated [CO₂], and it increased root biomass only under elevated [CO₂], while [CO₂] elevation increased total, stem, leaf and root biomass under high nutrient only. The high nutrient increased stem mass ratio (SMR) and decreased root mass ratio (RMR) under both [CO₂] while [CO₂] elevation reduced SMR under both nutrient treatments. [CO₂], nutrient and their interactions had no significant effects on leaf mass ratio, or leaf to root ratio. [CO₂] elevation reduced the leaf total N concentration and the effect was greater under low nutrient. [CO₂] elevation had no significant effect on leaf phosphorus (P) and potassium (K) concentration while the high nutrient treatment generally increased them.

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1. Introduction

The rise in atmospheric [CO₂] is one of the most pronounced global changes in the past 50 years (Prentice, 2001). Research has shown that [CO₂] elevation can have great impact on plants' growth and biomass production (Heath, 1997; Curtis and Wang, 1998; Ward and Strain, 1999). However, the magnitude of response often varies with soil nutrient conditions (Stitt and Krapp, 1999; Murray et al., 2000; Poorter and Pérez-Soba, 2001). The CO₂ enhancement of photosynthesis and biomass production is generally lower in nutrient-stressed than unstressed plants (Field et al., 1992; Kerstiens et al., 1995; Curtis and Wang, 1998; Ceentritto and Jarvis, 1999; Norby et al., 1999; Curtis et al., 2000; Murray et al., 2000; Poorter and Pérez-Soba, 2001). The differences are particularly strong in pot-grown plants and at extremely low nutrient availability (Tissue et al., 1993; Johnson et al., 1995). However, such

differences are generally not reflected in the biomass allocation between roots and shoots (Bosac et al., 1995; Gebauer et al., 1996; Tingey et al., 1996; Tissue et al., 1997).

Most of the previous studies have maintained the concentrations of other nutrient elements constant in different nitrogen treatments, and thus the ratios between N and other nutrient elements varied between treatments. Different nutrient elements can interact with each other in affecting plant functions (Kozłowski et al., 1991; Newbery, 1994; Gusewell, 2005). For instance, heavy N fertilization can induce K deficiency (Van den Driessche and Ponsford, 1995). It has been shown that foliage protein contents can decline as foliage N increases as a result of limitations by other nutrient elements, such as P, K or S (Brooks, 1986; Nakaji et al., 2001; Warrant and Adams, 2002). Since gene activity and protein synthesis related to photosynthetic enzymes are influenced by N:P ratios (Stitt, 1996; Nakaji et al., 2001), a curvilinear relationship between photosynthesis and foliar N concentration is often observed where P and K are not adjusted for N content in the fertilizer formulation (e.g., Manter et al., 2005) while a linear relationship is found where P and K are adjusted based on the amount of

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supplied N (Ripullone et al., 2003). Thus the effects of nitrogen can be confounded with the effects of nutrient ratios. In this study, we examined the responses of growth and biomass allocation in white birch seedlings (*Betula papyrifera* Mash.) to CO₂ elevation under low and high supplies of N, P and K where the ratios of N to P and K were kept constant between treatments.

White birch is a pioneer boreal tree species with a fast rate of juvenile growth and a relatively high nutrient demand (Burns and Honkala, 1990; Peterson et al., 1997). Since it has an indeterminate growth pattern, we hypothesize that under high nutrient conditions the growth of birch seedlings is limited by carbon but not by nutrient, and thus increasing [CO₂] (consequently photosynthetic production) and high nutrient supply will have synergistic effects on its growth and biomass production. Furthermore, since our earlier study did not detect photosynthetic down-regulation and thus inferred that the source-sink balance for carbon is maintained in white birch seedlings grown under low nutrient and elevated [CO₂] (Zhang and Dang, 2006), we hypothesize that the biomass allocation pattern between above-ground and below-ground organs will remain unchanged under different [CO₂] and soil nutrient conditions.

2. Materials and methods

2.1. Plant materials

White birch (*B. papyrifera* Mash.) seedlings were grown from seeds in the Lakehead University greenhouse under two CO₂ concentrations (i.e., ambient (360 ppm) and doubled (720 ppm)) in containers of 21 cm tall and 20.8 cm top diameter in February 2004. The growing medium was a mixture of peat moss and vermiculite (1:1, v/v). The seedlings were relatively uniform in size at the beginning of the experiment.

2.2. Experiment design

The treatments consisted of two CO₂ concentrations (ambient = 360 ppm; doubled = 720 ppm) and two levels of nutrient (i.e., low and high). The two CO₂ treatments were assigned to four greenhouses (replication = 2). The nutrient concentrations were 100 ppm N, 44 ppm P and 83 ppm K for the high nutrient treatment and 1/10 the strength of those levels for the low nutrient treatment (i.e., 10 ppm N, 4.4 ppm P and 8.3 ppm K). The foliar N concentrations for our high nutrient treatment correspond to the level found in natural white birch trees growing on nutrient rich sites as reported by Perry and Hickman (2001) while the values for our low nutrient treatment are 20–30% lower than the lowest levels found in the field (Perry and Hickman, 2001). The seedlings were fertilized to the dripping point twice a week. Other environmental conditions were set as follows for all the treatments: day/night temperatures 25–26 °C/16–17 °C from March to May, and 28–30 °C/18–20 °C starting in June, and photoperiod 16-h (the natural light was supplemented by high-pressure sodium lamps early mornings and late evenings). All the environmental

conditions were monitored and controlled using an Argus[®] controlling system (Vancouver, Canada). There were 10 seedlings in each treatment combination and they were about 3 cm tall at the time when the nutrient treatments started.

The volumetric moisture content of the growing medium was maintained around 50% as measured using a HH2 Moisture Meter and ML2X ThetaProbe (DELTA-T DEVICES, Cambridge, UK). The seedlings were watered up to twice a day during the summer to maintain the soil moisture condition. The experiment lasted about 3.5 months (from mid-February to early June, 2004).

2.3. Measurements of growth and biomass

The height and root collar diameter were measured at the end of the experiment on three seedlings that were randomly selected from the 10 seedlings of each treatment combination (per replication). The seedlings were then harvested and oven-dried at 70 °C for 48 h. The dry mass of leaf, root and stem was measured separately on an analytic balance. The leaf mass ratio (LMR = leaf mass/total seedling mass), root mass ratio (RMR = root mass/total seedling mass), and stem mass ratio (SMR = stem mass/total seedling mass) were used as indices of biomass allocation.

2.4. Leaf nutrient (nitrogen, phosphorus and potassium) assay

Three seedlings from each replication of each treatment combination were selected randomly 2.5 and 3.5 months after the start of the nutrient treatments and the 4th–6th fully expanded leaves from the apex were harvested. Total leaf nitrogen (N) concentration was assayed using the “Dumas Method” (McGill and Figueiredo, 1993), and phosphorus (P) and potassium (K) concentrations were assayed using the method of Kalra and Maynard (1998).

2.5. Statistical analysis

All the data were examined graphically for the normality of distribution (probability plots for residual analysis) and the homogeneity of variance (scatter plots) before the analysis of variance (ANOVA) was carried out. The above tests show that all the data satisfied the assumptions for ANOVA. When the ANOVA showed a significant interaction between nutrient and [CO₂], Scheffe's *F*-test for post hoc pairwise comparisons was conducted. All the analyses were carried out using the Data Desk statistical package (version 6.01, Data Description, Inc. 1996).

3. Results

3.1. Height, diameter and specific leaf area

[CO₂] had no significant effect on either height or root collar diameter growth ($P < 0.05$), but the high nutrient treatment significantly ($P < 0.001$) increased both growth parameters

Table 1

P-values of ANOVA for the effects of nutrient, [CO₂] and their interactions on height, root collar diameter, total tree biomass, component biomass, biomass ratios and specific leaf area of white birch seedlings

Source of variance	CO ₂	Nutrient	CO ₂ × nutrient
Height	0.3708	<0.0001	0.1259
Root collar diameter	0.2269	<0.0001	0.2542
Stem biomass	<0.0001	<0.0001	<0.0001
Leaf biomass	0.0002	<0.0001	0.0018
Root biomass	0.001	0.0028	0.0098
Total biomass	<0.0001	<0.0001	<0.0001
Stem mass ratio	0.0155	<0.0001	0.6255
Leaf mass ratio	0.9267	0.5158	0.4738
Root mass ratio	0.123	<0.0001	0.676
Specific leaf area	0.0008	<0.0001	0.8308

The seedlings were grown under two [CO₂] (360 and 720 ppm) and two levels of nutrient treatments (high and low) for about 3.5 months.

(Table 1 and Fig. 1). However, the [CO₂] elevation significantly ($P < 0.001$) decreased the specific leaf area while the high nutrient treatment increased it ($P < 0.001$, Table 1 and Fig. 1). There was no significant [CO₂]-nutrient interaction on any of the above morphological variables ($P < 0.05$).

3.2. Biomass

[CO₂] and nutrient treatment had significant interactive effects on the total biomass per tree and the biomass of individual organs ($P < 0.01$). The [CO₂] elevation significantly increased the total biomass, and stem, root and leaf biomasses only under the high nutrient, but not under low nutrient treatment (Table 1 and Fig. 2). While the high nutrient treatment significantly increased the total, stem and leaf biomass under both ambient and elevated [CO₂], it increased the root biomass only under elevated [CO₂] (Table 1 and Fig. 2).

3.3. Biomass ratios

The [CO₂] elevation significantly ($P < 0.05$) reduced stem mass ratio (SMR), but did not significantly affect the leaf mass ratio (LMR) or root mass ratio (RMR) (Table 1 and Fig. 3). The high nutrient treatment significantly increased SMR, reduced RMR, but had no significant effect on LMR (Table 1 and Fig. 3). There was no significant interaction between [CO₂] and nutrient on any of the mass ratios ($P < 0.05$).

3.4. Leaf nutrient concentrations

The [CO₂] elevation significantly decreased the leaf total nitrogen concentration only under the low nutrient treatment after 2.5 months' treatment, but reduced it under both nutrient treatments after 3.5 month's treatment (Table 1 and Fig. 4). The high nutrient treatment significantly increased the leaf N concentration in both measurements and under both ambient and elevated [CO₂], however, the effect was greater under the ambient than elevated [CO₂] after 2.5 months' treatment but this difference in response between CO₂ treatments disappeared after an additional month of treatment (Table 1 and Fig. 4).

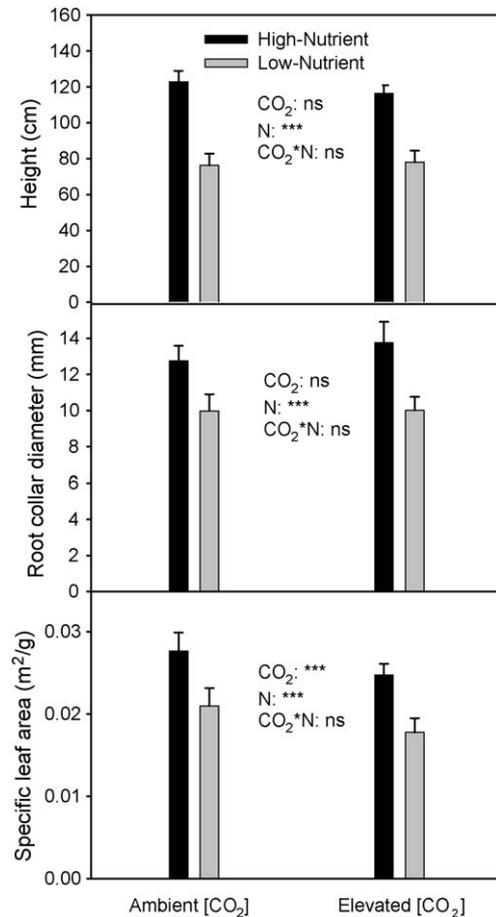


Fig. 1. Effects of [CO₂] and nutrient treatments on height, root collar diameter and specific leaf area (mean ± S.E.M.) of white birch seedlings. The seedlings were grown under two [CO₂] (360 and 720 ppm) and two levels of nutrient (high vs. low) for about 3.5 months. The significance levels (***) $P < 0.001$, ns = not significant) are based on ANOVA results. Scheffe's post hoc test was conducted where there was a significant interaction between [CO₂] and nutrient treatment. Means sharing the same letters are not significantly different from each other.

In contrast to its effects on leaf N, the CO₂ elevation did not significantly affect the leaf concentration of P or K. While the high nutrient treatment significantly increased leaf P concentration in both measurements, the effect on K only became significant after 3.5 months of treatment (Table 1 and Fig. 4).

4. Discussion

The data support our first hypothesis that under high nutrient conditions the growth of birch seedlings is limited by carbon but not by nutrient, and thus increasing [CO₂] (consequently photosynthetic production) and high nutrient supply will have synergistic effects on its growth and biomass production. While the high nutrient treatment generally increased the seedling total biomass and the biomass of leaf, stem and root, the enhancement was much greater under elevated [CO₂]. In fact, the nutrient effect on root biomass was only significant under the elevated [CO₂]. Likewise, the [CO₂] elevation increased the above biomass variables only under the high nutrient treatment. Our nutrient treatment protocol is different from those of other

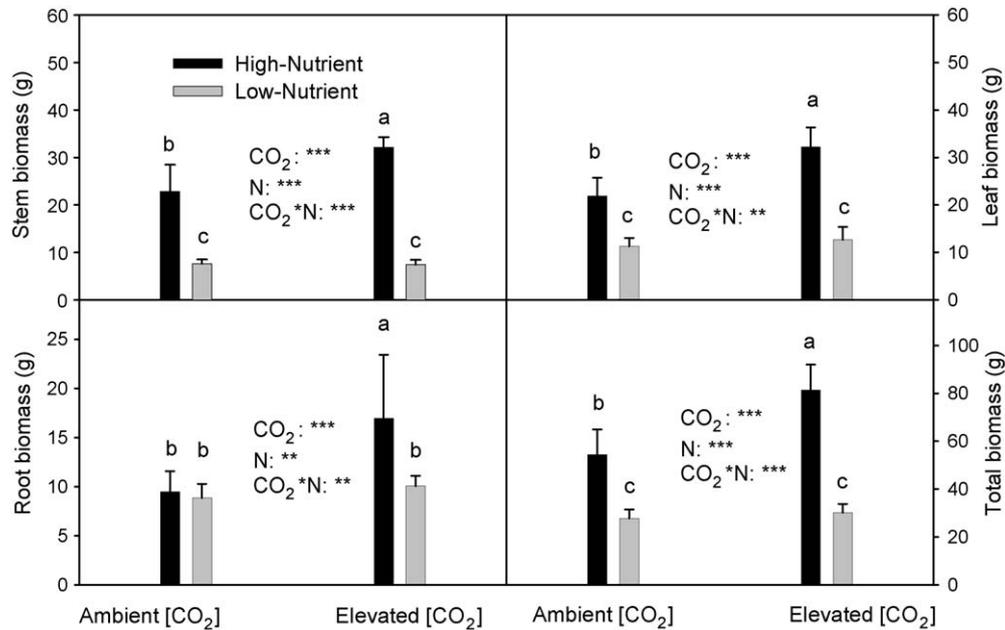


Fig. 2. Effects of [CO₂] and nutrient on the stem, leaf, root and total biomass (mean ± S.E.M.) of white birch seedlings. The significance levels (***) $P < 0.001$, ** $P < 0.01$ are based on the results of ANOVA and Scheffe's post hoc test. See Fig. 1 for other explanations.

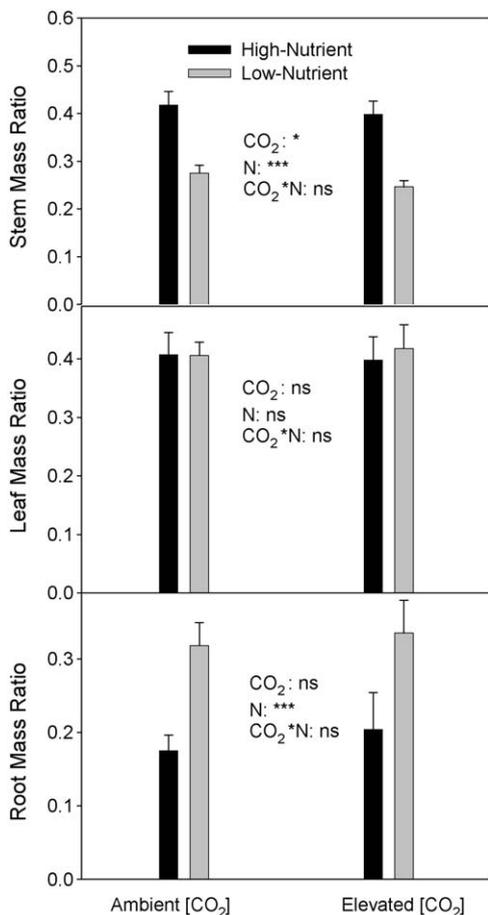


Fig. 3. Effects of [CO₂] and nutrient on the stem mass ratio, leaf mass ratio and root mass ratio of white birch seedlings. The significance levels (***) $P < 0.001$, * $P < 0.05$, ns = not significant) are based on the results of ANOVA and Scheffe's post hoc test. See Fig. 1 for other explanations.

studies in that we have maintained constant nutrient ratios between the different treatments while almost all other studies have maintained the concentrations of non-nitrogen nutrient elements constant between different treatments, in other words, the ratios between different nutrient elements varied between treatments. Research has shown that nutrient ratios can affect various plant functions. For instance, N:P ratio influences gene activity and protein synthesis related to photosynthetic enzymes (Stitt, 1996; Nakaji et al., 2001). A curvilinear relationship between photosynthesis and foliar N concentration is often observed where P and K are not adjusted for N concentration in fertilizer formulation (e.g., Manter et al., 2005) while a linear relationship is found where P and K are adjusted based on the amount of supplied N (Ripullone et al., 2003). However, despite the difference in the nutrient treatment protocol, our results are in a general agreement with the finding of other studies (e.g., Field et al., 1992; Murray et al., 2000; Poorter and Pérez-Soba, 2001) that the response of woody plants to [CO₂] elevation decreases as N availability decreases. These results support the argument that persistent increases in plant biomass production under elevated [CO₂] can only be maintained when N uptake is increased (Norby et al., 1986; Gifford, 1994; Soussana and Hartwig, 1996; Saxe et al., 1998). We speculate that young trees of other pioneer species with an indeterminate growth pattern, fast rates of juvenile growth and high nutrient demand would respond to CO₂ elevation and fertilization in a similar fashion as white birch did in this study. However, species with other shoot growth patterns may respond differently even when the nutrient ratios are kept constant.

The nutrient supply in our low nutrient treatment was too low for the trees to take advantage of the elevated [CO₂]. The foliar nitrogen concentrations of those trees were 20–30% lower than the lowest level found in natural white birch forests

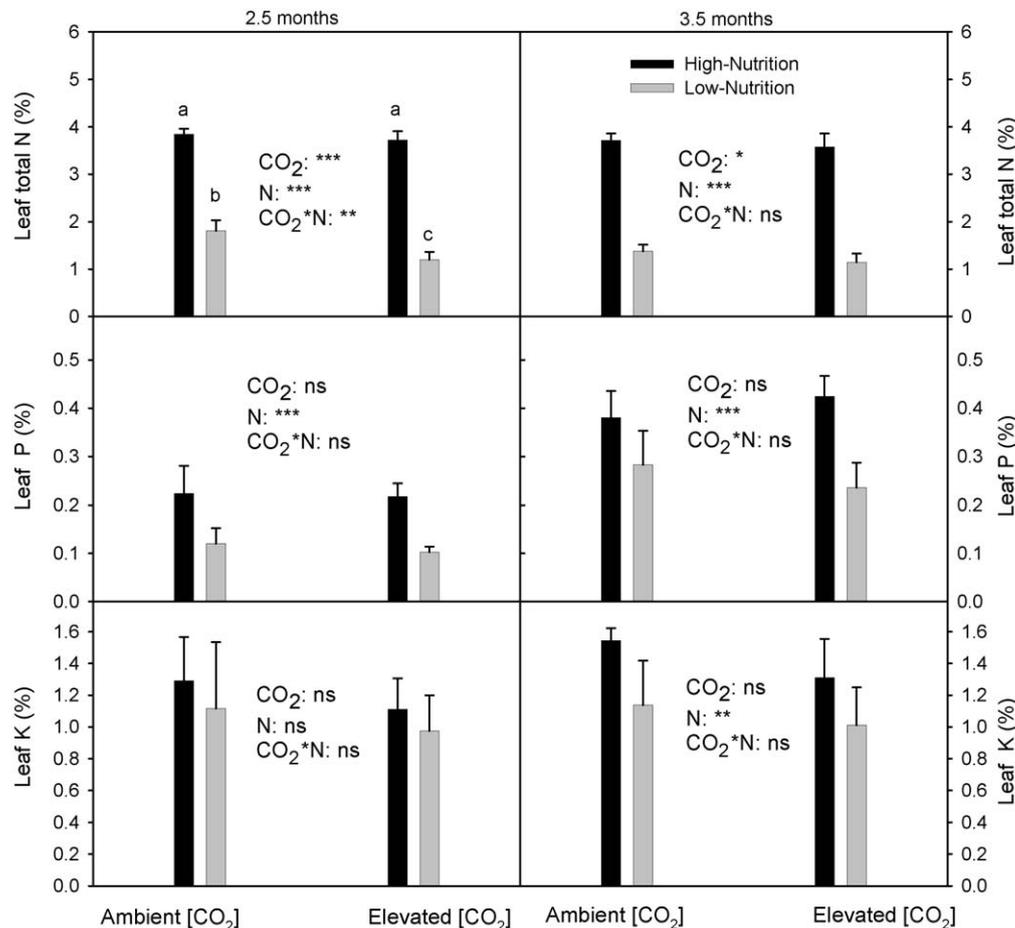


Fig. 4. Effects of $[CO_2]$ and nutrient on the leaf concentration of total nitrogen (N), phosphorus (P) and potassium (K) (mean \pm S.E.M.) of white birch seedlings. The significance levels (***) $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, ns = not significant) are based on the results of ANOVA and Scheffe's post hoc test. See Fig. 1 for other explanations.

(Perry and Hickman, 2001). The fact that the $[CO_2]$ elevation did not significantly increase the biomass accumulation in the low nutrient treatment suggests that the growth of those trees were nutrient limited, but not carbon limited. However, the $[CO_2]$ elevation did significantly decrease leaf nitrogen concentration. This decrease may reflect a diluting effect of $[CO_2]$ on leaf nutrient concentration. Photosynthetic rate generally increases in response to $[CO_2]$ elevation (Zhang and Dang, 2006; Saxe et al., 1998). However, if the increased production of carbohydrate cannot be utilized due to nutrient limitation to growth, carbohydrates will accumulate in the leaf, diluting nutrient concentration. The decrease of specific leaf area by $[CO_2]$ elevation can be considered as evidence for carbohydrate accumulation in the leaf and the consequent nutrient dilution. Our previous study has found that the low nutrient treatment indeed decreased the utilization of carbohydrate (Zhang and Dang, 2006). However, no significant $[CO_2]$ or $[CO_2]$ –nutrient interactive effects on leaf P or K concentration were detected in this study. It is also possible that there was an initial increase in growth in response to CO_2 elevation which diluted leaf N concentration, but such an increase was not sustained because nutrient became more limiting. This explanation is consistent with the viewpoint of Pettersson and McDonald (1994) that initial growth enhancement by $[CO_2]$ elevation will lead to more

rapid consumption of nitrogen within the pot and low nutrient supply cannot meet the requirement for further CO_2 stimulation. The fact that no significant CO_2 effect on growth or biomass was detected under the low nutrient treatment may simply indicate that the magnitude of the initial increase was too small to be detected in the final harvest. Similar findings have been reported for other species (e.g., Curtis et al., 2000; Maroco et al., 2002; Ainsworth et al., 2003).

Our results suggest that $[CO_2]$ elevation increased the biomass density of white birch seedlings. The most direct evidence to support this conclusion is the decrease in specific leaf area under elevated $[CO_2]$. Furthermore, the $[CO_2]$ elevation increased the stem biomass, but had no significant effects on the height or root collar diameter growth, suggesting an increase in biomass density of the stem. Wood density can influence the quality of the wood, such as pulp productivity and wood strength (Zhang, 1997). Additionally, changes in biomass density can have profound implications to the estimation of carbon stock and carbon sequestration of the forest. Thus, the effects of $[CO_2]$ elevation on biomass density warrant further, longer-term studies.

We hypothesized that white birch seedlings would not change the biomass allocation patterns under different $[CO_2]$ and soil nutrient conditions. This hypothesis is supported by the

leaf-to-root biomass ratio and shoot (leaf + stem) to root ratio data. These ratios are indicators of source-sink balance for carbohydrates and demand-supply balance for water (Lambers et al., 1998). The fact that [CO₂], nutrient or their interactions had no significant effects on either of these two ratios ($P < 0.30$) suggests that the seedlings maintained a source-sink balance and demand-supply balance under the different treatment conditions in this study. Furthermore, neither nutrient nor [CO₂] treatment had a significant effect on the leaf mass ratio and the [CO₂] elevation did not significantly affect the root mass ratio. These results are in agreement with the finding of other researchers that [CO₂] does not change the biomass allocation between roots and shoots (Bosac et al., 1995; Gebauer et al., 1996; Tingey et al., 1996; Tissue et al., 1997; Curtis and Wang, 1998). However, the low nutrient treatment did significantly increase the root mass ratio, supporting the theory that low nutrient supply stimulates biomass allocation to roots (e.g., Larcher, 2003; Walker and Gessel, 1990; Marschner, 1995).

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