Various growth strategies of yellow birch seedlings in multiple-abiotic factor changing environments

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ABSTRACT

Elevated CO_2 concentration, light intensity and soil-sterile conditions are thought as three of the most important factors to affect plant growth and development. However, their combined physiological effect on plants is unknown so far. In this study, we measured the possible individual and combined impacts of the three factors on the growth of yellow birch seedlings (*Betula alleghaniensis* Britton). Our results showed that from individual perspective, elevated CO_2 can significantly increase biomass attributes (e.g., leaf, root, and stem) and root biomass ratio; light intensity can significantly influence traits like total biomass and leaf biomass; while soil conditions can influence traits like height and leaf biomass. From two-way interaction perspective, the interaction CO_2 and soil can significantly influence total plant biomass, root biomass and R:S ratio; the interaction of light and soil significantly influenced the height, basal diameter, stem biomass, and so on; the interaction between CO_2 and light did not significantly influence the plant growth parameters except for branch biomass ratio. From three-way interaction perspective, both traits stem biomass and root biomass were influenced by the co-effect of the three environmental factors. In conclusion, single or interactive effects among CO_2, light intensity and soil conditions can lead to various growth strategies for the yellow birch.

Keywords: elevated CO_2; interaction; light; soil nutrition; yellow birch seedlings

Both models and measurements predict that the concentration of atmospheric carbon dioxide (CO_2) will increase exponentially from 388 Pa of the present time to the value around 470–940 Pa by the 2100 (Schneider 2001). In relation to this, forest dynamics will change, especially in the regions of middle and high latitudes in northern hemisphere (Oren et al. 2001), and a better understanding for the responses of seedling stage to changing resources is critical for providing insights into the effects of global climate change on forest ecosystem functioning.

Increasing CO_2 concentration affected the biomass change, and this difference is larger during the early stages of tree development in different natural resources (Bazzaz and Miao 1993). It resulted in dramatic increases in root growth and root biomass (Saxe et al. 1998) (such as dry weigh and turnover) regardless of species concerned or study conditions (Pregitzer et al. 1995). In many instances, roots exhibit the greatest relative dry weight gain among plant organs under high CO_2 (Rogers et al. 1995). It was also expected to increase the root:shoot ratio (R:S ratio) to improve acquisition of belowground resources (Saxe et al. 1998). Under elevated CO_2, the source-to-sink balance within plants changes more rapidly than that under ambient CO_2 levels. Carbon transportation and partitioning under elevated CO_2 trend to be sink-controlled. Plant growth, while enhanced under elevated CO_2, may

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be limited (possibly genetically). Moreover, most responses of tree seedlings to elevated CO_2 are to increase aboveground growth and biomass, for instance, stem base area and leaf weight (DeLucia et al. 1999), while others found slight decline in aboveground allocation (Zak et al. 2008).

Light and soil environment need to be considered when one attempts to model CO_2 effects on forest succession (Kerstiens 2001). On one side, releasing plants from light competition would allow a relatively large response to elevated CO_2 (Agrell et al. 2000), whereas others argued that relative growth with elevated CO_2 were larger in low light than high light (Bazzaz and Miao 1993, McDonald et al. 1999). Meanwhile, elevated CO_2 increased seedling dry mass in relative high-nutrient soil condition (Saxe et al. 1998, Zak et al. 2008), a majority of which might be located belowground (Sefcik et al. 2007). Biomass allocation adjustments in response to CO_2 availability should be less significant or absent when soil resources are non-limited. On the other side, light availability was known to cause more photosynthate allocation in the roots for mycorrhizal formation, and mycorrhizal colonization, mycelium and spore production in soil were also positively correlated with light (Bethlenfalvay and Pacovsky 1983). Among studies investigating interactions between elevated CO_2 and soil nutrients, the majority focused on the nitrogen supply rates, few people researched the effects of soil-sterilize condition related to mycorrhizal colonization, microbial activity and soil nutrients. Furthermore, how the biomass allocation was affected by elevated CO_2 in sterilized soil? How about the interaction of changeable light density and elevated CO_2 on the life strategy and biomass allocation of seedlings? All these were poorly understood.

Yellow birch (*Betula alleghaniensis* Britton) is an ectomycorrhizal (ECM) species that is moderately shade-tolerant. In southwestern Quebec, Canada, Yellow birch is an important plant species due to the high economic value. However, plenty of individuals died in their middle-age, even if they grew well in their seedlings. This study was mainly aimed to address the following research questions: (a) What's the combined effect of increased CO_2, light and soil-sterilized condition on the growth of Yellow birch seedlings, of which, autoclaving soil was proved to kill mycorrhizal fungi and decreases microbial activity, resulting in a soil nutrient flush (Packer and Clay 2000); and (b) which factor combined with elevated CO_2 has the most positive influence on the growth of Yellow birch during its succession stage? We hypothesized that seedlings under the single/combined effect of light availability, CO_2 concentration and soil condition should present different strategies of biomass allocation. We also expected that this shade-tolerant species may change its growth characteristics under elevated CO_2, and different soil condition and light availability.

MATERIALS AND METHODS

Experimental design. The experiment was conducted as a completely randomized design with two CO_2 concentrations, three light levels and two soils in the McGill University Phytotron in Canada. Two of the chambers (multi-function TC30 chambers, Controlled Environments Limited, Winnipeg, Canada) were maintained at 350 (S.E. < ± 10) and two others at 700 (S.E. < ± 10) ppm CO_2 concentrations. However, the four chambers could not be used randomly for the two CO_2 levels. In the chambers, fluorescent lamps were used for plant growth. Their spectral photon distribution ranged within photosynthetically active radiation and the ration between red light and far-red light was around 1:2, similar to the natural daylight condition. In each of the growth chambers, three light levels (46.62, S.E. ± 0.93; 122.92, S.E. ± 2.46; 417.66, S.E. ± 9.49 μmol/m^2s) were established. The low and medium light levels were created by 78 cm wide × 130 cm long frames covered by two or four layers of black colored shade and nylon cloths. For the high light level, plants were placed on a platform (78 cm wide × 130 cm long × 25 cm high) without shading in each chamber. Based on the average full sunlight of 1600 μmol/m^2s measured in a dominant yellow birch forest at Rivičre ŕ Pierre in the Réserve Faunique de Portneuf 47°04'N and 72°15'W, Québec, Canada, the relative light of the three levels were calculated as 2.9%, 7.7% and 26.1% to mimic closed, small, and large canopy gaps in natural forests (≤ 5% > 5%–< 10%, and > 20% of full sunlight). Those lights represented either diffusion irradiation in closed and small gaps or mean irradiation of direct and diffuse light in a large gap. For the growing medium, natural soil was collected from the A_1H horizon of the Duchesnay Forest in Québec, Canada. The soil was an ortho-humo-ferric podzol with the average pH of 5.4 and average NO_3 content of 2.917 mg/g, NH_4 of 35.513 mg/g, P of 0.072 mg/g, Ca of 0.381 mg/g, K of 1.970 mg/g and Mg of 0.151 mg/g. After removing stones and coarse root fragments, and homogeneous mixture, the soil was stored in a cold room at 4°C before use. In the experiment, half of the soil was sterilized

by autoclaving three times for 20 min at 15 psi. Under each light level, 4 seedlings grown in each of soil types were randomly placed. The 4 growth chambers were used twice for 4 replications of each treatment.

Plant and germination. Yellow birch seeds were obtained from the Québec Ministry of Natural Resources. The germination rate and dry-weight percentage of the seeds were 72.5% and 75.8% respectively with a high relative growth rate (Villar et al. 1998). Yellow birch seeds were germinated twice, in January and April. Before the germination, the seeds were placed in a beaker and covered with water for 20 days at room temperature. The water in the beaker changed every week. After the soaking period, yellow birch seeds were sown in propagation plug trays (28 cm wide × 55 cm long × 6 cm high, Plant Products Co. Ltd, Brampton, Canada). Each tray contained 72 plugs (6 rows × 12 columns) filled with the natural soil. The trays of the seeds were placed in the McGill university greenhouse with a 16 h photoperiod and 25/15 (S.E. ± 3/2)°C daytime/nighttime temperatures for germination. In the greenhouse, these seedlings were watered once per week and grew in the greenhouse for 64 days. Before being placed in the growth chambers, the seedlings were transplanted to 12 cm diameter × 12 cm high pots with a 3 cm diameter hole each in the bottom, and kept in the greenhouse for a further 3 days to minimize the disturbance and mortality due to environmental change after the transplantation.

Environment of growth chamber. In all of the growth chambers, the air temperature, the relative humidity and the photoperiod were maintained at 25/15 (S.E. ± 0.05/0.04)°C daytime/nighttime, 60/65% (S.E. ± 0.86/0.58) in daytime/nighttime, and 16 h (6:00 a.m. to 10:00 p.m.). During the light period, the light gradually increased to the maximum and decreased to zero in order to mimic sunrise and sunset, and minimize the potential disturbance of plant processes by changing the light suddenly. Under the high light, all the plant pots were covered by aluminum foil with a 3 cm diameter hole at the center to reduce the possible increase in soil temperature by heat energy from the lights in the chambers. The foil was approximately 2 cm above the soil surface in the pots so as not to affect ventilation, soil humidity, and soil respiration. The soil temperatures under the high and low lights were monitored by thermometers, and the difference during the experiment ranged from 0.5 to 1°C. All the pots under each of the light levels in each growth chamber were placed in a tray that was 120 cm long × 60 cm wide × 10 cm high. The trays were filled with 4 cm of water, which was automatically taken up by the capillarity of the soil in the pots. Soil moisture under the different light treatments in each chamber was monitored by soil moisture meters with wet, medium and dry marks. When the meter arrows pointed to the medium mark, water was filled up to the 4 cm height again in all the trays.

At the beginning of the treatment, the initial height and basal diameter of each of the seedlings were measured. After 55 days, the height and diameter of the seedlings had responded to the elevated CO_2 based on the measurement of 20 seedlings selected randomly in each chamber. All the seedlings grew in the chambers for 62 days.

Harvesting. After the light measurement, 96 yellow birch seedlings were harvested, and half of them were from 350 and 700 Pa CO_2 chambers. Among these seedlings, 16 seedlings were taken from each of the low, medium, and high light levels at each of the CO_2 levels. The leaves, stem (including branches), and root system of each seedling were separated. The roots were washed using tap water.

Growth traits investigated. Initial and final height, initial basal diameter, stem biomass, leaf biomass, root biomass were measured. The organ biomass was weighed using a digital balance after drying at 70°C for 48 h. Total plant biomass, root (biomass) to shoot (biomass) ratio, stem biomass ratio (defined as the rate of stem biomass to total plant biomass), leaf biomass ratio (defined as the rate of leaf biomass to total plant biomass), branch biomass ratio (defined as the rate of branch biomass to total plant biomass), root biomass ratio (defined as the rate of root biomass to total plant biomass) were calculated.

Data analyses. Analysis of covariance (ANCOVA) was used to test effects of elevated CO_2, light, soil and their interactions on all of the investigated traits. Initial tree height and initial basal diameter significantly affected all the organ and plant growth (Cheng 2007); thus, both initial variables were used as covariates to remove their effects on the analyses.

All the examined traits were graphically examined for normality using histograms and for homogeneity of variance using scatter plots. If necessary, these traits were transformed logarithmically. All the data were tested to satisfy the assumptions for ANCOVA analysis. SPSS (version 10) statistical software (SPSS Inc. Chicago, USA) was used to perform the analyses.

Table 1. Analyses of covariance for effects of elevated CO_2, light, soil and their interactions on height, basal diameter, total biomass, stem biomass, leaf biomass, branch biomass, root biomass, root to shoot ratio, stem biomass ratio, leaf biomass ratio, branch biomass ratio, root biomass ratio. Initial height and initial basal diameter are as covariates to remove the size effects on the data (± S.E.); *P* – probability. Different letters are significant difference at $P < 0.05$

Sources	CO_2 (C)		Light (L)			Soil (S)		C × L	C × S	L × S	C × L × S
	360 ppm	700 ppm	low	middle	high	NS	S	(*P*)			
Height	45.424[a] ± 1.227	45.332[a] ± 1.261	44.836[a] ± 1.485	45.827[a] ± 1.505	45.471[a] ± 1.568	42.944[a] ± 1.314	47.812[b] ± 1.359	0.210	0.650	0.001	0.477
Base diameter	4.794[a] ± 0.099	4.973[a] ± 0.101	3.972[a] ± 0.119	4.635[a] ± 0.121	6.043[b] ± 0.126	4.755[a] ± 0.106	5.012[a] ± 0.109	0.153	0.346	0.005	0.706
Total biomass	8.920[a] ± 0.313	10.254[b] ± 0.321	5.108[a] ± 0.378	7.951[b] ± 0.384	15.703[c] ± 0.400	9.315[a] 0.335	9.860[a] 0.346	0.413	0.016	0.102	0.092
Stem biomass	1.321[a] ± 0.053	1.502[b] ± 0.055	0.976[a] ± 0.065	1.256[a] ± 0.066	2.003[b] ± 0.068	1.363[a] ± 0.057	1.460[a] ± 0.059	0.775	0.103	0.000	0.043
Leaf biomass	3.522[a] ± 0.128	3.902[b] ± 0.131	1.933[a] ± 0.155	3.263[b] ± 0.157	5.941[c] ± 0.163	3.397[a] ± 0.137	4.028[b] ± 0.142	0.502	0.658	0.053	0.942
Branch biomass	0.644[a] ± 0.056	0.659[a] ± 0.047	0.377[a] ± 0.086	0.399[a] ± 0.047	1.178[b] ± 0.049	0.568[a] ± 0.054	0.735[a] ± 0.059	0.411	0.387	0.028	0.429
Root biomass	3.533[a] ± 0.180	4.291[b] ± 0.185	2.067[a] ± 0.218	3.052[a] ± 0.221	6.617[b] ± 0.230	4.087[a] ± 0.193	3.737[a] ± 0.199	0.094	0.001	0.013	0.013
Root to shoot ratio	2.785[a] ± 0.243	3.289[a] ± 0.250	2.870[a] ± 0.294	2.629[b] ± 0.298	3.612[b] ± 0.310	3.143[a] ± 0.260	2.930[a] ± 0.269	0.637	0.965	0.307	0.094
Stem biomass ratio	15.968[a] ± 0.468	15.560[a] ± 0.480	17.929[a] ± 0.566	15.983[b] ± 0.574	13.382[c] ± 0.598	15.232[a] ± 0.501	16.296[a] ± 0.518	0.859	0.873	0.075	0.265
Leaf biomass ratio	40.578[a] ± 0.836	39.028[a] ± 0.859	38.161[a] ± 1.012	42.310[b] ± 1.025	38.937[a] ± 1.068	38.133[a] ± 0.896	41.473[b] ± 0.926	0.095	0.790	0.184	0.060
Branch biomass ratio	6.044[a] ± 0.381	5.803[a] ± 0.320	5.563[a] ± 0.585	4.501[ab] ± 0.319	7.708[b] ± 0.330	8.318[a] ± 0.366	6.530[a] ± 0.402	0.027	0.056	0.011	0.517
Root biomass ratio	38.896[a] ± 1.075	40.896[b] ± 1.105	42.138[a] ± 1.302	37.344[b] ± 1.319	40.205[b] ± 1.374	42.633[a] ± 1.152	37.159[b] ± 1.191	0.415	0.639	0.400	0.066
Root to above-ground ratio	0.625[a] ± 0.038	0.692[a] ± 0.031	0.609[a] ± 0.057	0.635[a] ± 0.032	0.731[a] ± 0.033	0.697[a] ± 0.036	0.620[a] ± 0.039	0.446	0.034	0.152	0.728

RESULTS

Effects of main factors. Elevated CO_2 significantly increased total plant biomass, stem biomass, leaf biomass, root biomass and root biomass ratio (Table 1).

Different light conditions have generated different results for various plant attributes. For example, low light significantly increased root to shoot ratio, stem biomass ratio, branch biomass ratio and root biomass ratio compared to middle and high light conditions. Middle light increased total plant biomass, leaf biomass and leaf biomass ratio. High light increased basal diameter, total plant biomass, stem biomass, leaf biomass, branch biomass and root biomass; decreased stem biomass ratio, and leaf biomass ratio compared to those in middle and low lights (Table 1).

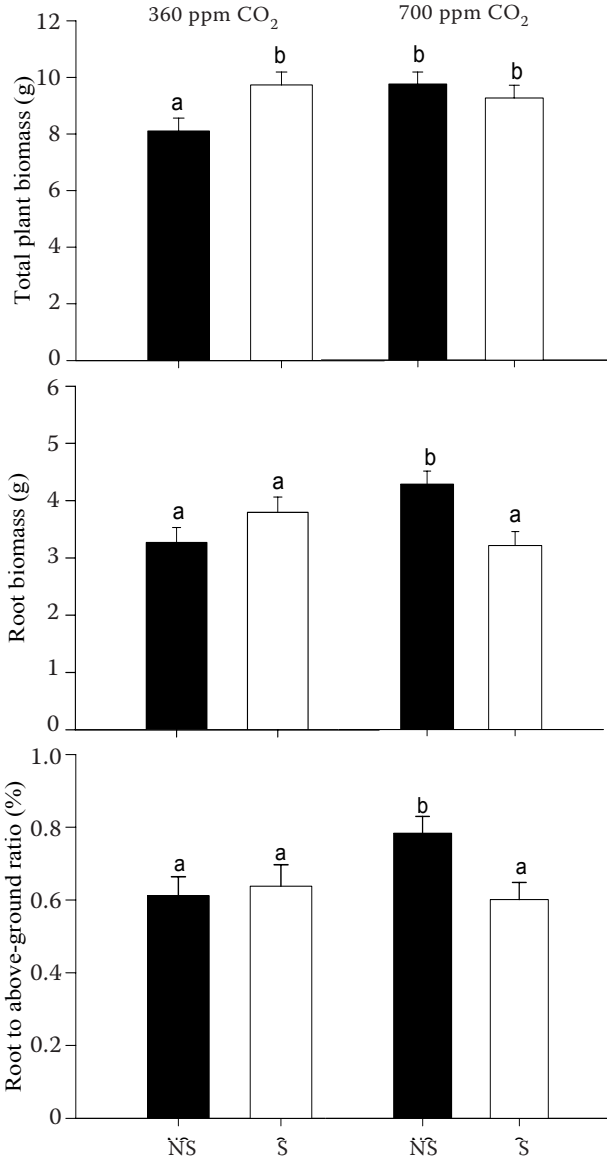

Figure 1. Interactive effects of CO_2 (350, 700 ppm) × soil (NS for non-sterile soil, S for sterile soil, and defined as the same for other Figures) on total plant biomass and root biomass in the seedlings. The numbers of samples are 96 and 92 from 350 and 700 ppm CO_2. Among them, 96 and 92 samples are harvested from non- and sterile soil. The numbers are the same as for other Figures

Sterile soil significantly increased height, leaf biomass, leaf biomass ratio; decreased root biomass ratio (Table 1).

Interactive effects of two-way factors. There were interactive effects among the three resources in influencing plant growth (Table 1). But, interaction between CO_2 and light did not significantly influence the plant growth parameters except for branch biomass ratio (Table 1), which demonstrated a highest value under high light treatment (Figure 3). It should also be noticed (Figure 3) that branch biomass ratio did not decrease with the decrease of light density, as the lowest value was observed under medium light treatment whether CO_2 concentration was elevated or not.

In contrast, total plant biomass, root biomass and R:S ratio were all significantly influenced by the interaction of CO_2 and soil (Table 1). Sterile soil increased total plant biomass growing in both ambient and elevated CO_2, whereas non-sterile soil only increased the total plant biomass under elevated CO_2 (Figure 1). Figure 1 also indicated that increase of root biomass and R:S ratio was noticeable only in non-sterile soil with elevated CO_2.

Interaction of light × soil significantly influenced the height, basal diameter, stem biomass, branch biomass, root biomass and branch biomass ratio of Yellow Birch (Table 1). They were all higher in sterile soil with middle light, but some parameters, including stem and root biomass, became smaller in sterile soil when the light was elevated (Figure 2). When light was low, insignificant differences between sterile and non-sterile soil were observed for most of the parameters, except for a lower height and a higher branch biomass in sterile soil.

Interactive effects of the three-way factors. Stem biomass and root biomass were significantly affected by the interaction of CO_2 × light × soil. From the upper plot of Figure 4, the stem biomass was highest in non-sterile soil with high light and CO_2 concentration, followed by the non-sterile and sterile soil with ambient CO_2 and low light, and then followed by the sterile soil with higher light. The lower plot of Figure 4 indicated that biomass allocation in root was benefited from high light condition regardless of the soil and CO_2 conditions.

DISCUSSION

Of the three environmental factors, light has the greatest effect on seedlings growth. Two-way interactions between CO_2 and light, CO_2 and soil, light and soil on plant growth were significant, and the response to light strength was depended on soil condition.

Responses of plant growth strongly to interaction of CO_2 and soil. Total plant biomass and root biomass was increased under elevated CO_2 in non-sterile soil. The total biomass between non-

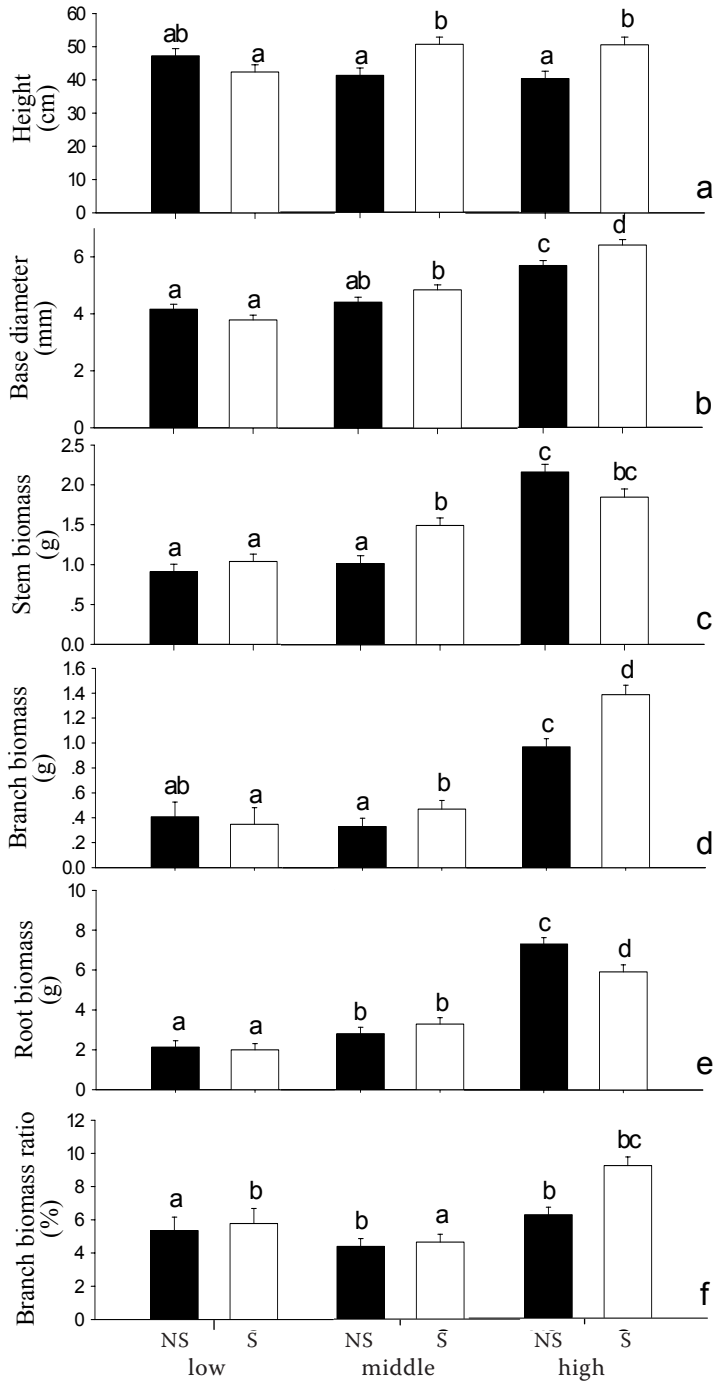

Figure 2. Interactive effects of light (low, middle, high) × soil on height, base diameter, stem biomass, branch biomass, root biomass and branch biomass ratio

sterile soil and sterile soil treatments under elevated CO_2 presented no significant difference, whereas the root biomass for the different soil treatments showed a remarkable significant difference. We suggested that the increase of photosynthetic rates in response to elevated CO_2 resulted in a concomitant increase in total biomass when nutrients were unlimited. Similar results have been reported for other species (Bazzaz and Miao 1993, Murray et al. 2000). This also supported the point that down-regulation of photosynthesis is often related to insufficient nutrient supply rates (Pettersson and McDonald 1994). At elevated CO_2, root biomass allocation remarkably decreased maybe related to the decrease of mycorrhizal fungi, other soil biota and soil nutrients (Packer and Clay 2000) in sterile soil. As some studies have confirmed that mycorrhizas increased the root access and improved the nutrition and growth of host plant (Smith and Smith 1996). Our result not only supported this point, but also found that even under elevated CO_2, root exploration or length density decreased when microbial activity and mycorrhizas decrease. The R:S ratio of seedling under elevated CO_2 is increased when soil is sterilized, suggesting that seedlings grow may shift biomass

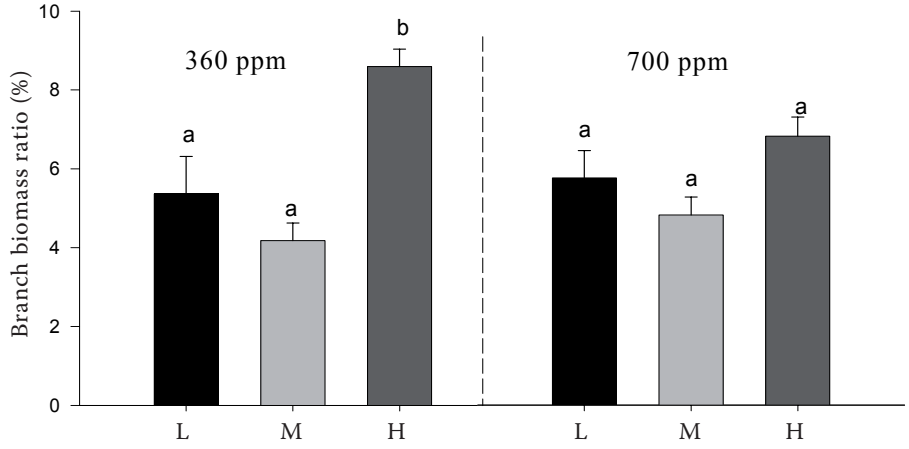

Figure 3. Interactive effects of CO_2 and light on branch biomass ratio

allocation away from leaves and wood in favor of roots. Furthermore, this indicated a potential short-term reduction in above-ground net primary productivity, similar to the previous works from Murray et al. (2000) on Sitka spruce (*Picea sitchensis* (Bong.) Carr.). Kolek and Kozinka (1991) demonstrated that R:S would increase under mineral nutrients deficiency condition in order to increase their root surface absorption capacity, which was not supported when CO_2 is elevated in our research. As Yin et al. (2008) suggested, that high R:S strategy can decrease the risk of seedling damage or mortality when stochastic exposure to environmental stresses in response to future climate change.

Plant growth responses to interaction of CO_2 and light. The branch biomass ratio in high light was higher than that in low and middle light under low CO_2, whereas high CO_2 reduced the branch biomass ratio in high light (Figure 3). McDonald et al. (1999) found that starch of paper birch (*Betula papyrifera* Marsh.) increased by 440% under the elevated CO_2 (69.6 ± 0.2 Pa) and high light (855 μmol/m^2 s), but the growth was carbon-limited below the level available in the elevated CO_2-high light treatment, they

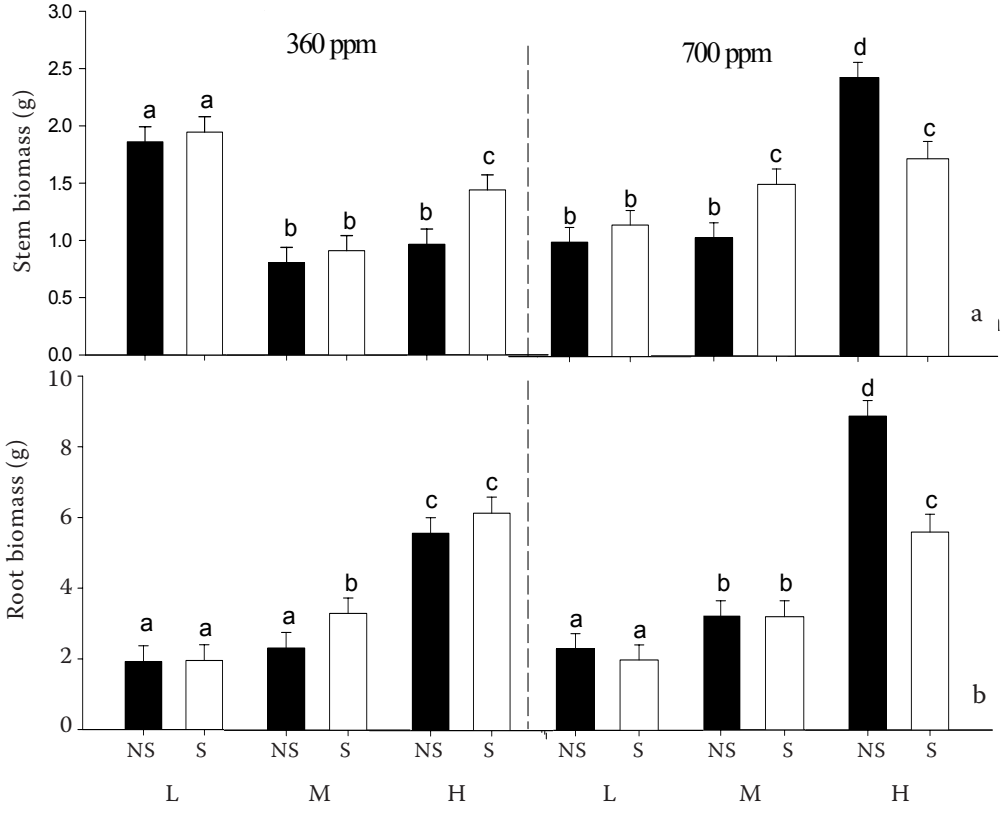

Figure 4. Interactive effects of CO_2 × light × soil on root biomass and stem biomass

also found that elevated CO_2 increased plant growth and allocation to foliar secondary metabolites, and the responses to CO_2 were strongly enhanced by increasing light availability. Agrell et al. (2000) also found that effects of enriched CO_2 were strongest in high light, which resulted in an average increase of 79% in starch content, compared to an average increase of 66% in low light on paper birch. But, opposite results were also found in some studies. Osborne et al. (1997) demonstrated that the relative CO_2 effects may be particularly large in deep shade because higher CO_2 concentrations reduce photorespiration and, thus, decrease the light compensation point of photosynthetic carbon uptake. In line with this, Bazzaz and Miao (1993) also found the relative CO_2-stimulation of biomass production was increased at low light levels in temperate forest tree seedlings. Our research did not find the similar uptrend as the above study, but light environment needs to be considered when species are ranked according to their responsiveness to CO_2 concentration (Kerstiens 2001) and this magnitude of changes may differ among tree species (Agrell et al. 2000).

Plant growth strongly responded to interaction of soil and light. Height growth is an indicator of fitness as it is usually correlated with biomass increase. Over the duration of our experiment, seedling height in sterile soil was increased by the light intensity, but the opposite tendency was observed in non-sterile soil. This can be explained that high light intensity compensated the deficient of soil nutrients and seedling selected the growth strategy of developing the height so as to increase light capture capability, which may lead to greater production of photosynthates and promote ectomycorrhizal development (Cheng et al. 2005).

In addition, high light increased stem, branch biomass and root biomass at both soil treatments. However, stem biomass and root biomass increased more under high light in non-sterile soil, whereas diameter, height, branch biomass and branch biomass ratio increased more under high light in sterile soil. This suggested that high light interact with non-sterile soil trended to increase C assimilation of seedling xylem while high light interact with sterile soil trended to develop the plant morphological traits. In addition, root biomass under high light in non-sterile soil increased more than that in sterile soil. While Bazzaz and Miao (1993) found even greater differences (6 times) in gray birch (*Betula populifolia*), this showed that high light stimulated microbial activities in non-sterile soil and enhanced mycorrhizal colonization and therefore, resulted in the increase of root density and biomass. Walters and Reich (2000) suggested that as light was increased, shade-tolerant species tend to have better growth with greater soil nutrients. Increasing light can increase leaf carbohydrate levels, resulting in higher translocation to the roots (Hodge et al. 1997), and then the development promotion of mycorrhizal and rhizosphere associations (Cheng et al. 2005). Even there were no significant changes on total biomass, our results based on root biomass and stem diameter still supported this contention, but the interactive effects of light, soil nutrients and mycorrhizal colonization may differ from that caused by different light quality and species.

Stem biomass and root biomass primarily responded to the interaction of three-way factors. During the experiment, stem biomass significantly changed after adding the resource of CO_2 from the treatment of light and soil, which supported the research results of Cheng (2007) on the same species. As CO_2 elevated, the greatest value of stem biomass in high light and non-sterile soil was changed from the non-sterile soil which interacted with low light in ambient CO_2. This suggested that elevated CO_2 promoted the interactive effects of high light and non-sterile soil and resulted in the greatest stem biomass, which can lead to height growth for capturing more light (Cheng 2007). Furthermore, stem biomass in non-sterile soil and high light presented a greater increase than that in sterile soil and high light, since that the elevated CO_2 evenly made better assimilation of soil nutrients to stem with enough mycorrhizal colonization attached. Conversely, stem C assimilation is highly restricted if light resource is limited, even the soil resource is under elevated CO_2 condition.

Root biomass had the similar fluctuating tendency at elevated CO_2 under high light. Nonetheless, the elevated CO_2 had no significant effects on root biomass allocation under low light, and root biomass somehow changed when plants are grown in sterile soil under middle light. Under elevated CO_2, increased light seemed to pronouncedly increase leaf carbohydrate levels, such as starch and sugars which may result in higher translocation to the roots (Hodge et al. 1997), and sequentially enhance the exudation of sugars, amino acids, amides and phenolic acids to the soil (Grayston et al. 1996), this can further promote the development of mycorrhizal and rhizosphere associations (Cheng et al. 2005) and root growth. Another possible reason might be the increase of growth in lateral roots since the initiation of new lateral roots depends on irradiance, which also promotes the growth of roots biomass.

Acknowledgments

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