

White birch has limited phenotypic plasticity to take advantage of increased photoperiods at higher latitudes north of the seed origin

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ABSTRACT

Global warming induced northward migration will expose trees to longer photoperiod regimes during the growing season. The phenotypic ability of trees to take advantage of the longer photoperiods and elevated atmospheric CO₂ concentration ([CO₂]) will likely be a critical factor for determining their success and performance at the new locations. We investigated how growth, biomass, and biomass allocations respond to the interactive effects of photoperiod regimes and [CO₂] in white birch (*Betula papyrifera* Marsh.). Seedlings were exposed to ambient (400 μmol mol⁻¹) or elevated concentration (1000 μmol mol⁻¹) [CO₂], and four photoperiod regimes corresponding to 48 (seed origin), 52, 55, and 58°N latitude for two growing seasons. Our results show that growth, biomass, and biomass allocation were affected by photoperiod regime but not by [CO₂]. Seedling growth and biomass were stimulated by the three photoperiod regimes north of the seed origin. Plants under the photoperiod regime of 52°N were 15% higher in growth and 18% higher in biomass than under the photoperiod regime of the seed origin (48°N). However, increases in photoperiod regimes beyond that of 4° north of the seed origin did not lead to an additional increase in growth and biomass. The differences in biomass components among the three longer photoperiods were statistically insignificant, but the leaf biomass and stem biomass were higher under the longer photoperiods relative to the seed origin. While the differences between two adjacent photoperiods were not always statistically significant during the two growing seasons, biomass allocated to roots showed a general decreasing trend with increases in photoperiod from the seed origin to 58°N latitude. Our results suggest that despite the limited plasticity in growth and biomass displayed in much higher latitudes, white birch will likely benefit from the longer photoperiod regimes during the growing season associated with migration or seed transfer to higher latitudes.

1. Introduction

The predicted shift in tree species distribution in response to the ongoing climate change requires the successful establishment of seedlings in the new location which depends on, among other factors, the physiological and/or morphological plasticity of the species or population to acclimate to the climatic and edaphic conditions of the new location which may have positive or negative effects survival and growth (Chen et al., 2011; Pitelka and Group, 1997). For example, a northward range shift of tree species in quest of suitable habitat will expose them to new photoperiod regimes. Photoperiod regimes can have a significant influence on the survival, growth, and productivity of trees and influence the distribution of tree species (Thomas and Vince-Prue, 1996). Therefore, a good understanding of how changes in photoperiod regimes may interact with the future, elevated atmospheric CO₂ concentration in affecting the growth, biomass and biomass

allocations of trees, particularly in the context of climate-change-induced migration, will likely be critical for understanding and predicting the distribution, composition and productivity of future forests (Saikkonen et al., 2012).

The CO₂ concentration in the atmosphere has increased dramatically in the last century and will continue to increase for the rest of this century (Pachauri et al., 2014). The increase in atmospheric [CO₂] generally enhances the photosynthetic activities and growth of C₃ plants and influences biomass allocations (Ceulemans and Mousseau, 1994; Curtis and Wang, 1998; Rogers et al., 1994). Under elevated [CO₂], plants often tend to increase dry matter allocation to roots, particularly when water or nutrient resources are limited (Curtis and Wang, 1998; McGuire et al., 1995; Rogers et al., 1995; Saxe et al., 1998; Stulen and Den Hertog, 1993). While the influence of [CO₂] elevations on biomass allocation can be influenced by other environmental factors, such as photoperiod regimes, research in this area is generally scarce,

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particularly in the context of climate change induced northward migration of boreal trees.

In the temperate and boreal zones, photoperiod controls various physiological and phenological processes/traits and serves as an environmental cue for the synchronization of plants' phenological and physiological processes with the seasonal climate conditions (Salisbury, 1981; Thomas and Vince-Prue, 1996; Lambers et al., 2008; Jackson 2009). A change in photoperiod regime can affect the growth and productivity of tree species in different ways. Photoperiod can influence growth and productivity via its effect on the timing of photoperiod-controlled phenological events such as bud burst in the spring and bud formation in autumn (Basler and Körner, 2012; Junttila and Kaurin, 1990; Velling, 1979). Photoperiod can also alter plant growth rate and biomass production (Hay 1990, Thomas and Vince-Prue 1996). Longer photoperiods have been reported to stimulate growth (Oleksyn et al., 1992; Johnsen and Seiler, 1996) and the rate of biomass accumulation (Stinziano and Way, 2017). Increases in leaf area and leaf mass ratios and specific leaf area have also been reported for plants grown under extended photoperiods (Adams and Langton, 2005; Hay, 1990). Photoperiod can also affect the biomass allocation between aboveground and belowground organs in trees (Li et al., 2015). However, the results on the photoperiod influence over the biomass allocation in trees vary with species and other factors, and past studies are primarily focused on coniferous trees, grass and herbaceous species (Bigras and Daoust, 1993; Burdett and Yamamoto, 1986; Hay, 1990; Heide, 1974; Heide et al., 1985; Stinziano and Way, 2017). Furthermore, the combined effect of two or more interacting factors is generally different from the summation of their individual effects. For example, it is unknown how much of the stimulation of carbon allocation to roots by $[\text{CO}_2]$ elevations (McGuire et al., 1995) can be offset by the opposite effect of longer photoperiods associated with a northward migration (Gestel et al., 2005; Hamilton et al., 2016; Johnsen and Seiler, 1996). Therefore, a good understanding of such potential interactive effects may play an important role in predicting the success of northward migration of tree species under a changing climate.

White birch (*Betula papyrifera* Marsh.) is a widely distributed pioneer tree species in North America (Burns et al., 1990; Farrar, 1995). It requires high water and nutrient supplies and grows rapidly in the juvenile stage (Simard and Vyse, 1992). This study investigated the interactive effects of photoperiod regime and CO_2 elevation on the growth and biomass allocation of white birch in the context of climate change induced migration. We exposed white birch seedlings to the photoperiod regimes at 48 (seed origin), 52, 55, and 58°N latitudes and two CO_2 concentrations ($400 \mu\text{mol mol}^{-1}$ and $1000 \mu\text{mol mol}^{-1}$). We have tested the following hypotheses: (1) CO_2 elevation will increase the overall seedling growth and biomass allocation to roots; (2) A longer photoperiod will stimulate aboveground growth and increase biomass allocation to the shoot; and (3) CO_2 elevation and longer photoperiod will cancel each other's effect on biomass allocation between shoot and roots because their effects are opposite of each other.

2. Materials and methods

2.1. Plant materials

Catkins of white birch (*Betula papyrifera* Marsh) were collected from 12 natural trees in Thunder Bay (48.4215°N, 89.2619°W). The seed trees were at least 115 m apart from each other and from the same population. Seeds were extracted manually, air dried and stored in plastic bags at room temperature before sowing. The experiment was conducted at the Lakehead University Forest Ecology Complex in Thunder Bay. Seeds were germinated in a tray (50 cm × 25 cm) filled with peat moss and vermiculite (1:1, v:v). During the germination, the temperature and photoperiod were set to 22/16 °C day/night and 16 h day-length, respectively. Seedlings of relatively uniform size (2 cm average height) were transplanted into pots of 12 cm deep and 12/

9.5 cm top/bottom diameter filled with a mixture of vermiculite and peat moss (1:3, v:v).

2.2. Experimental design

The treatments consisted of two $[\text{CO}_2]$ (ambient 400 and elevated $1000 \mu\text{mol mol}^{-1}$) and four photoperiod regimes corresponding to 48 (seed origin), 52, 55, and 58°N latitude in a split-plot design with $[\text{CO}_2]$ as the whole plot and photoperiod regime as the split-plot. There were 20 seedlings per treatment combination. The CO_2 elevation was achieved using natural gas CO_2 generators (model GEN-2E; Custom Automated Products Inc., Riverside, California, USA). Each $[\text{CO}_2]$ was replicated twice using independently environment-controlled greenhouses. The photoperiod in each greenhouse was adjusted weekly to emulate the weekly average regime of the growing season for the longest photoperiod of the four treatments, and that photoperiod regime was shortened by manually applying black-out shade to emulate the photoperiod regime for each of the other three treatments. A wooden frame was established around each split-plot to facilitate the shading and to maintain consistency across treatments. High-pressure sodium lamps (P.L. Systems, Grimsby, ON, Canada) was used to extend the natural photoperiod when the natural day-length in the greenhouse was shorter than required. The air temperatures were derived from the 10-year weekly averages of Environment Canada records for the seed origin location (Environment Canada, 2016). The temperature in each greenhouse was ramped at four set points at 4:00, 10:00, 16:00, and 22:00 h according to the 10-year average temperatures for the corresponding hour. The experiment was carried out for two growth cycles. The first cycle emulated the environmental conditions of June 7 to November 15 and the second cycle emulated the conditions of April 26 to November 12. The dates mentioned in the rest of the paper refer to the dates that were emulated.

The $[\text{CO}_2]$, temperature, and humidity were controlled using an Argus Titan Environment-control system (Argus Control Systems Ltd, Vancouver, BC, Canada). During the growing period, the water content of the growing medium was maintained around 50–60% of the field capacity as determined using an HH2 Moisture Meter and ML2X Theta Probe (DELTA-T DEVICES, Cambridge, UK). All the seedling were fertilized twice a week with a fertilizer solution containing 50/81/30.3 mg L^{-1} of N/P/K from April 26 to May 25; 150/65.2/125 mg L^{-1} N/P/K at the rapid growth phase (May 26 to August 30); and 50/54.3/156.3 mg L^{-1} N/P/K during the hardening phase (September 1 to 25) (Plant Products Co Ltd, Brampton, Ont., Canada). The fertilizer application was discontinued on September 25. The seedlings were all cold hardened and set buds at the end of the growing season when the environment conditions in the greenhouses were emulating the average natural environmental conditions of mid-November for the region as described previously. The dormant seedlings were moved to a dark cold storage room (-4°C) where they were kept for 5 months and 11 days before the initiation of the second growing season when the average natural environmental conditions for the region were emulated starting from those of April 26. The seedlings were transferred into bigger pots (18 cm deep, 16/14 cm top/bottom diameter) in the second growing season but the treatments were otherwise identical in the two growing seasons.

2.3. Growth and biomass measurement

We measured seedling height and root collar diameter on five randomly chosen seedlings per treatment combination per replication at the end of each growth cycle when the buds were fully formed, 267 Julian days (around the autumnal equinox, no significant difference among different photoperiod treatments). Following growth measurement, the seedlings were harvested and separated into leaves, stems, and roots. The total leaf area (LA) per seedling was determined using WinFolia (Regent Instrument Inc., Quebec, Canada). The samples were then oven dried at 70°C for 48 h and weighed on an analytical balance

(0.001 g precision) to determine biomass for leaf, stem and root. We then calculated the specific leaf area (SLA = leaf area/dry leaf mass), leaf area ratio (LAR = total leaf area/seedling dry mass), root to shoot

ratio (R:S = root mass/shoot mass), leaf mass ratio (LMR = leaf mass/seedling dry mass), stem mass ratio (SMR = stem mass/seedling mass), and root mass ratio (RMR = root mass/seedling mass).

Table 1

Summary of ANOVA (*P*-value and Degree of freedom (DF)) for the effects of [CO₂], photoperiod regime, and their interactions on height (H), root-collar diameter (RCD), biomass components, total plant biomass, biomass ratio, and leaf area ratio (LAR) and specific leaf area (SLA). Seedlings were subjected to two [CO₂] (400 and 1000 μmol mol⁻¹) and four photoperiod regimes (corresponding to 48, 52, 55, and 58°N latitude) for two growing seasons in environment-controlled greenhouses. Significant (*P* ≤ 0.05) and marginal significant (*P* ≤ 0.1) *P*-values are bolded.

Variable		2017			2018		
		[CO ₂]	Photoperiod	[CO ₂] × Photoperiod	[CO ₂]	Photoperiod	[CO ₂] × Photoperiod
H	<i>F</i>	7.866	13.439	0.201	1.74	5.096	0.063
	<i>P</i>	0.107	0.005	0.892	0.318	0.044	0.978
RCD	<i>F</i>	0.201	3.151	8.372	1.128	2.892	0.226
	<i>P</i>	0.218	0.015	0.213	0.399	0.124	0.875
Leaf	<i>F</i>	1.335	11.385	0.669	1.272	8.498	5.833
	<i>P</i>	0.367	0.007	0.601	0.377	0.014	0.033
Root	<i>F</i>	0.175	1.119	0.248	1.708	2.308	0.014
	<i>P</i>	0.716	0.413	0.86	0.321	0.176	0.998
Stem	<i>F</i>	2.765	8.246	0.395	2.537	6.374	0.322
	<i>P</i>	0.238	0.015	0.761	0.252	0.027	0.810
Total biomass	<i>F</i>	1.026	5.343	0.460	1.977	4.65	0.549
	<i>P</i>	0.418	0.039	0.720	0.295	0.052	0.667
Shoot	<i>F</i>	2.063	9.472	0.471	1.908	6.406	1.175
	<i>P</i>	0.287	0.011	0.713	0.301	0.027	0.395
LMR	<i>F</i>	0.120	4.944	0.051	0.654	10.794	7.181
	<i>P</i>	0.762	0.046	0.983	0.504	0.008	0.021
SMR	<i>F</i>	0.206	11.969	0.058	0.714	5.964	1.725
	<i>P</i>	0.694	0.006	0.980	0.487	0.031	0.261
RMR	<i>F</i>	0.226	12.217	0.054	1.068	5.525	1.283
	<i>P</i>	0.682	0.006	0.982	0.41	0.037	0.362
RS	<i>F</i>	0.232	12.268	0.056	0.895	6.127	1.378
	<i>P</i>	0.678	0.006	0.981	0.444	0.029	0.337
LAR	<i>F</i>	0.211	2.748	0.184	1.553	0.62	0.849
	<i>P</i>	0.691	0.135	0.904	0.339	0.627	0.516
SLA	<i>F</i>	0.038	0.151	0.575	0.919	1.463	0.544
	<i>P</i>	0.864	0.925	0.652	0.439	0.316	0.670
DF		1	3	3	1	3	3

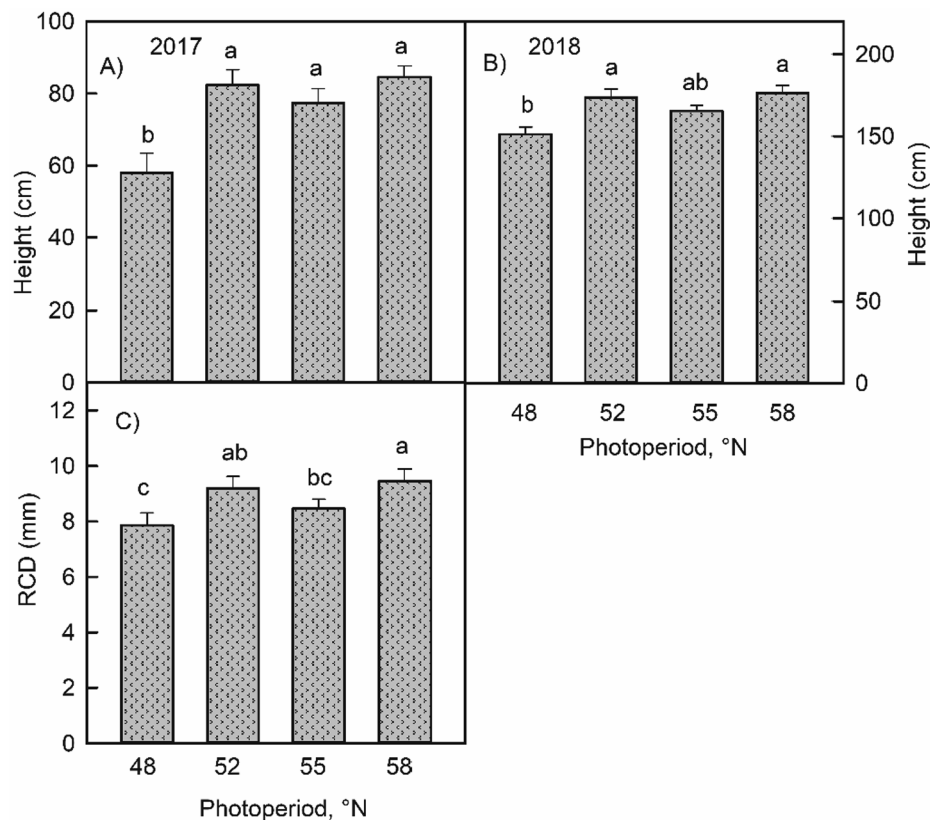


Fig. 1. Total height and root-collar diameter (RCD) in white birch seedlings in 2017 (left panel) and in 2018 (right panel) growing seasons. Seedlings were grown under the photoperiod regimes corresponding to 48° (seed origin), 52°, 55°, and 58°N latitude and under 400 (ambient) and 1000 μmol mol⁻¹ CO₂ (elevated) for two growing seasons. Data are presented as Mean ± SE (N = 20: 5 seedlings per treatment combination × 2 replications per combination; the data were pooled for the [CO₂] treatment because the interaction was not significant, 5 × 2 × 2 = 20). Means with different letters for each measurement time are significantly different from each other (*P* ≤ 0.1, Fisher's LSD).

2.4. Statistical analysis

Statistical analyses were performed using the R program (v. 3.5.0, R Core Team 2018). Photoperiod, [CO₂] and their interactive effects were tested by two-way analysis of variance (ANOVA). The two levels of CO₂ (n = 2) were randomly assigned to the whole plots (four greenhouses) as a completely randomized design (CRD) and the sub-plots (n = 4) were treated as nested within the whole plot in ANOVA. ANOVA was run separately for the two growth cycles. The total number of individuals (N) was 80: 5 seedlings per treatment combination, 2 levels of CO₂ with 2 replicates each, and 4 photoperiods nested within CO₂. Mean differences were considered significant at $P \leq 0.05$ and marginally significant at $P \leq 0.1$. Significant differences among photoperiod regimes and significant interactions were further evaluated using the Fisher's LSD test. The data were transformed before analysis using the power transformation to meet the assumption of normality and homogeneity.

3. Results

3.1. Growth and biomass production

Growth and biomass were not affected by [CO₂] (Table 1). The height of seedlings grown under the three photoperiod regimes north of the seed origin was generally significantly greater than that under the photoperiod regime of the seed origin (Table 1, Fig. 1A and B). The response pattern of seedling diameter was similar to that of height in the first growing season (Fig. 1C), but the differences became statistically insignificant in the second growing season (Table 1).

Leaf biomass was significantly affected by photoperiod regime and the response patterns were different between the two growing seasons: it generally increased with increasing latitude from the seed origin in the first growing season (Table 1, Fig. 2A), but the response to photoperiod regime was significantly affected by [CO₂] in the second growing season (Table 1). Under the elevated [CO₂], leaf biomass was smaller at 52°N than other photoperiods; Under the ambient [CO₂], leaf

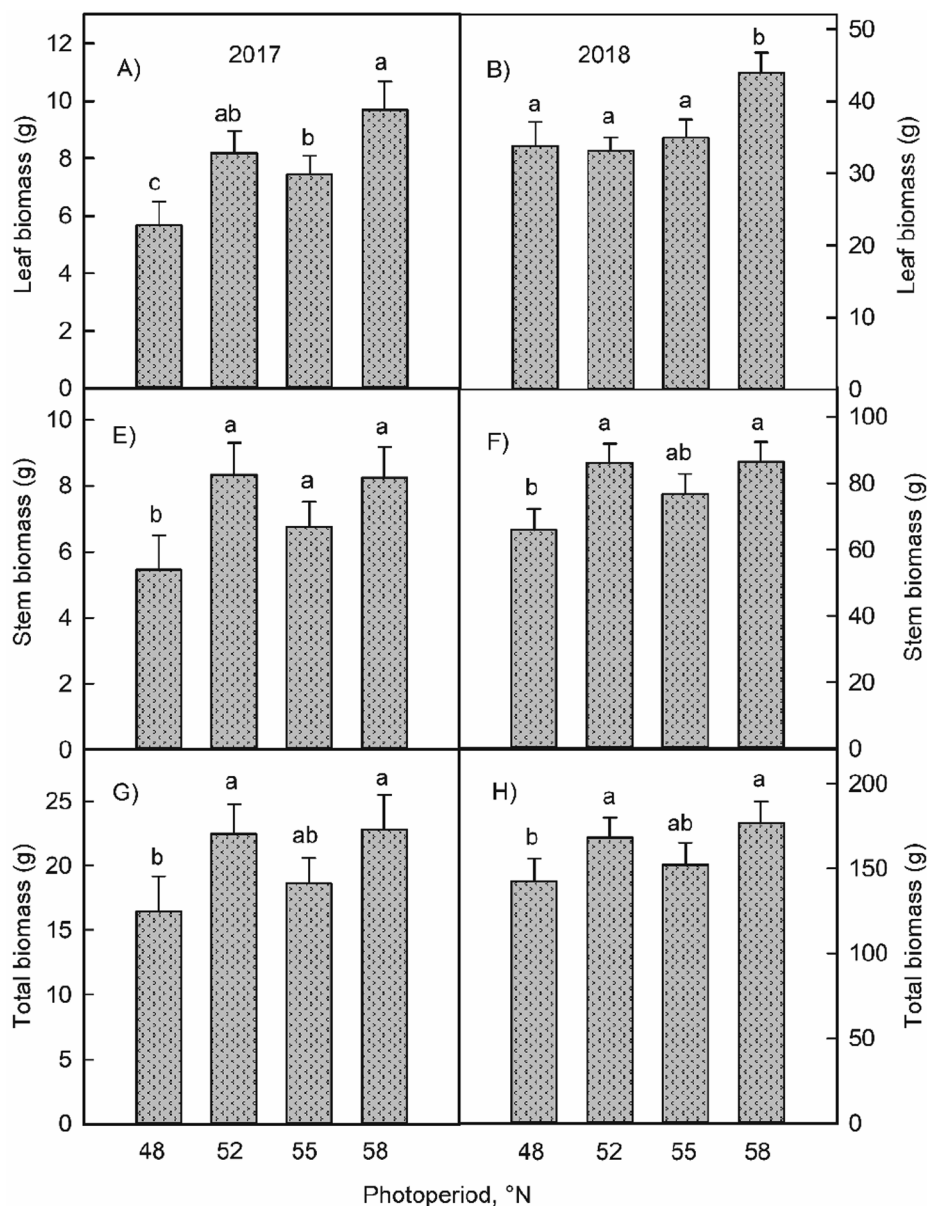


Fig. 2. Leaf biomass, stem biomass and total plant biomass of white birch seedlings as affected by photoperiod regime in 2017 (left panel) and 2018 (right panel) growing seasons. Data are presented as Mean \pm SE ($N = 20$ as explained in Fig. 1). Means with different letters indicate significantly different from each other ($P \leq 0.05$, Fisher's LSD). See Fig. 1 for more explanations.

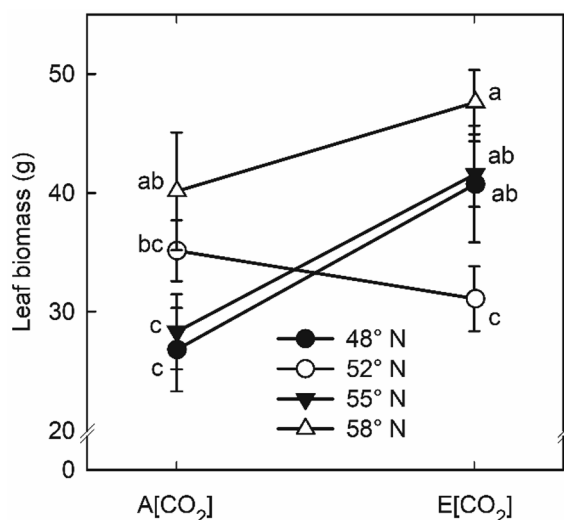


Fig. 3. Leaf biomass of white birch seedlings as affected by photoperiod regime and [CO₂] (ambient, A[CO₂]; elevated, E[CO₂]) in 2018 growing season. Data are presented as Mean \pm SE ($N = 10:5$ seedlings per treatment combination $\times 2$ replications per combination). Means with different letters indicate significantly different from each other ($P \leq 0.05$, Fisher's LSD). See Fig. 1 for more explanations.

biomass was greater at 52 and 58° N than at the other photoperiod regimes (Fig. 3). Further, the [CO₂] elevation generally enhanced leaf biomass at all photoperiod except at 52° N (Fig. 3).

Root mass was not significantly affected by any of the treatments in either of the growing seasons (Table 1). The stem biomass and total seedling biomass at the seed origin were generally smaller than those at the photoperiod regimes at higher latitudes with the exception of 55° N at which the stem and total seedling biomass were not significantly different from those at the seed origin (Fig. 2E-H). However, no significant differences were detected among the photoperiod regimes at 52, 55, and 58° N latitude on stem or total biomass in either growing season (Fig. 2E-H).

3.2. Biomass allocation

Photoperiod regime significantly affected biomass allocation to leaf, stem, and roots (Table 1). In the first growing season, the leaf mass ratio (LMR) under the photoperiod regime of 58° N was significantly greater than under the photoperiod of the seed origin and 52° N primarily at the expense of reduced root mass ratio (RMR, Fig. 4A). The stem mass ratio (SMR) under the photoperiod regime of the seed origin was significantly lower than those under other photoperiod regimes (Fig. 4A). The response patterns, however, changed in the second growing season (Fig. 4B): LMR was significantly smaller under the photoperiod of 52° N than under the other three photoperiod regimes, and the SMR at 52 and 55° N was significantly greater than the seed origin. Also, the biomass allocated to leaf was lowered by the photoperiod of 52° N under elevated [CO₂] and the [CO₂] elevation increased this parameter at 48° N but decreased it at 52° N (data not shown). The biomass allocation to roots and root/shoot ratio decreased with increases in latitude, but the difference between 52 and 55° N, or between 55 and 58° N were insignificant (Fig. 4A-D).

4. Discussion

Our results supported the hypothesis that longer photoperiods would stimulate growth and increase biomass allocation to above-ground parts but did not support the hypothesis that [CO₂] elevation would offset the effect of longer photoperiods on biomass allocation.

The results suggest that the photoperiod regime of 4° north of the seed origin (52 vs. 48° N) increased the growth and biomass of white birch. However, further increases in photoperiod regimes associated with even higher latitudes did not lead to much further increase in growth, suggesting that white birch may not be able to take advantage of longer photoperiods in the growing season at much higher latitudes. The seedlings grown under the photoperiod regime 4° north of the seed origin latitude were 15% higher in growth and 18% higher in biomass than the seedlings grown under the photoperiod regime of the seed origin. However, there was no significant difference either in seedling growth or biomass between 52° N and the two higher latitudes. Although, the contribution of leaf biomass weakened at the final harvest for plants grown under 52° N, increased total seedling biomass at longer photoperiods was primarily attributed to increases in stem biomass and leaf biomass. At the end of the experiment period, we observed a net increase in shoot biomass (leaf + stem) of 20% at 52° N, 5% at 55° N and 9% at 58° N latitude, as compared to the seed origin. The corresponding increases in total light period during the growing season at the three latitudes were 65, 107 and 116 h, respectively. Apparently, more hours of light did not lead to much further increase in growth. While the positive responses in growth and biomass to longer photoperiods found in this study are in general agreement with the results on other tree species in the literature (Abeli et al., 2015; Bigras and Daoust, 1993; Johnsen and Seiler, 1996), this is the only study that has identified the magnitude of increase in photoperiod at which the maximum phenotypic plasticity is reached. Oleksyn et al. (1992) have reported significant increases in height growth and total biomass when scots pine (*P. sylvestris* L.) is grown under a photoperiod regime corresponding to a 10° increase in latitude from the seed origin. Similar results are found in a field experiment by Schreiber et al. (2013) where trembling aspen (*Populus tremuloides* Michx.) is moved 7° north from the latitude of the seed origin (54 vs. 47° N).

The most likely reason for the increased growth of white birch grown under longer photoperiods is the lengthened periods of photosynthesis and subsequent increases in carbohydrate production (Stinziano and Way, 2017). There are several mechanisms for growth increases under longer photoperiods. Longer photoperiods can expedite budburst and leaf expansion in the spring (Basler and Körner, 2012; Thomas and Vince-Prue, 1996) and delay leaf senescence in the fall (Raulo, 1976; Velling, 1979; Viherä-Aarnio et al., 2005), leading to a longer growing season. In this study, the longer photoperiods did not affect the timing of leaf senescence in the fall (Tedla et al., unpublished). However, the spring budburst did occur earlier at 55 and 58° N than at 48 and 52° N under the elevated [CO₂], but the trend was opposite under the ambient [CO₂] (Tedla et al., unpublished). Longer photoperiods can also increase biomass and growth by increasing leaf area ratio and specific leaf area (Adams and Langton, 2005; Hay, 1990), but photoperiod did not significantly affect either of them in this study. Longer photoperiods can affect the decline of photosynthetic capacity during summer to autumn transition as the photoperiod becomes shorter and temperatures become lower (Bauerle et al., 2012). The physiological measurements of this study show that the photoperiod regimes of 55 and 58° N latitude generally did not stimulate photosynthetic rate (relative to the seed origin) under the elevated [CO₂] but substantially increased photosynthetic rate under the ambient [CO₂] (Tedla et al., unpublished). Stinziano and Way (2017) also suggest that both the longer hours of photosynthesis and increased efficiency of light energy conversion into biomass are major contributors to the increased growth of white spruce (*Picea glauca* (Moench) Voss) under a longer photoperiod regime. However, the current and other controlled-environment studies cannot give any indication on the effects of the declined solar elevation and increased lateral shading within and between trees at higher latitudes on the physiology, phenology and growth of trees in the field.

Growing under longer photoperiod regimes reduced the biomass allocation to roots in white birch. Although the differences between two

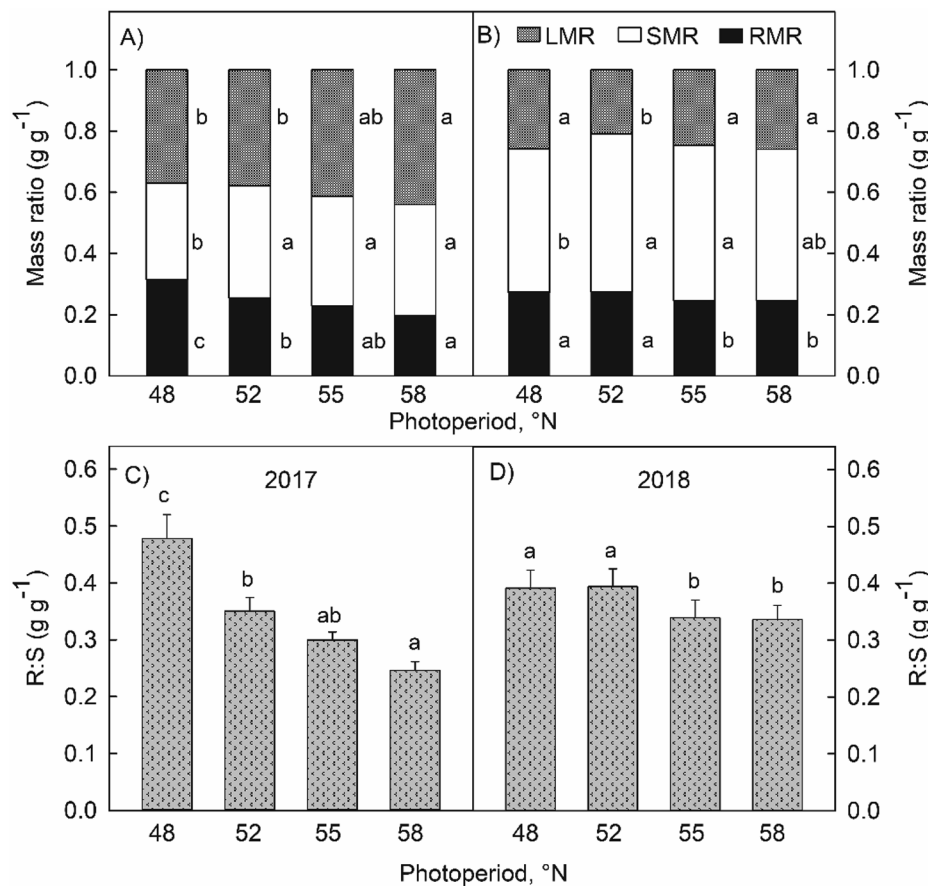


Fig. 4. Leaf, stem and root mass ratios (A and B) and root to shoot ratio (C and D) of white birch seedlings as affected by photoperiod regime. Left panel and right panels indicate 2017 and 2018 growing seasons, respectively. Data are presented as Mean \pm SE ($N = 20$ as explained in Fig. 1). Means with different letters indicate significantly different from each other ($P \leq 0.05$, Fisher's LSD). See Fig. 1 for more explanations.

adjacent treatment levels were not always statistically significant, there is a general trend that the proportion of biomass allocated to roots declined with increases in photoperiods associated with increases in latitude from 48 (seed origin) to 58°N. This trend seems counter-intuitive. Since longer photoperiods increase carbohydrate production as stated previously, growth should become more limited by water and nutrients from the soil, and logically, the biomass allocation to roots should increase rather than decrease. However, all the seedlings were well watered and supplied with ample of nutrients in this study. Presumably, the trees did not experience drought or nutrient stress in any of the treatments. It is, therefore, reasonable to conclude that the decrease in root mass ratio with increasing photoperiods reflected the stimulation of shoot growth by the increased carbohydrate production in trees growing under longer photoperiods (Keyes and Grier, 1981). However, because of the relatively small sample size and short term nature of this study, this study may not have been able to detect all the changes in biomass allocation to aboveground parts. Nevertheless, the leaf mass ratio and stem mass ratio were significantly higher under the photoperiod regime at 58°N than the seed origin (48°N). Similar trends are reported for other tree species, e.g., *P. glauca* (Bigras and Daoust, 1993), lodgepole pine (*Pinus contorta* Dougl.) (Burdett and Yamamoto, 1986), and Norway Spruce (*Picea abies*) (Heide, 1974). However, there are also results in the literature that photoperiods have no effects on biomass partitioning (Burdett and Yamamoto, 1986; Stinziano and Way, 2017).

White birch has an indeterminate growth pattern and is highly plastic in morphology and physiology in response to environmental conditions (Ashton et al., 1998; Li et al., 1996; Wang et al., 1998). Although the main effect of photoperiod on growth and biomass allocation were mostly significant, the interactive effect of photoperiod and [CO₂] was generally statistically insignificant in this study. Our results suggest that white birch may benefit from the longer photoperiods

associated with a northward migration or seed transfer of up to 4° north of the seed origin. However, the current study is a short-term greenhouse experiment on a single population of the species. There may be variations in the response between different populations. Therefore, larger scale studies are warranted to investigate possible genetic variations in the response.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2019.117565>.

References

- Abeli, T., Orsenigo, S., Guzzon, F., Faè, M., Balestrazzi, A., Carlsson-Granér, U., Müller, J.V., Mondini, A., 2015. Geographical pattern in the response of the arctic-alpine *Silene suecica* (Caryophyllaceae) to the interaction between water availability and photoperiod. *Ecol. Res.* 30, 327–335.
- Adams, S.R., Langton, F.A., 2005. Photoperiod and plant growth: a review. *J. Hort. Sci. Biotechnol.* 80, 2–10.
- Ashton, P.M.S., Olander, L.P., Berlyn, G.P., Thadani, R., Cameron, I.R., 1998. Changes in leaf structure in relation to crown position and tree size of *Betula papyrifera* within fire-origin stands of interior cedar-hemlock. *Can. J. Bot.* 76, 1180–1187.

- Basler, D., Körner, C., 2012. Photoperiod sensitivity of bud burst in 14 temperate forest tree species. *Agric. For. Meteorol.* 165, 73–81.
- Bauerle, W.L., Oren, R., Way, D.A., Qian, S.S., Stoy, P.C., Thornton, P.E., Bowden, J.D., Hoffman, F.M., Reynolds, R.F., 2012. Photoperiodic regulation of the seasonal pattern of photosynthetic capacity and the implications for carbon cycling. *Proc. Natl. Acad. Sci. USA* 109, 8612–8617.
- Bigras, F., Daoust, A., 1993. Influence of photoperiod on shoot and root frost tolerance and bud phenology of white spruce seedlings (*Picea-Glauca*). *Can. J. For. Res.-Rev. Can. Rech. For.* 23, 219–228.
- Burdett, A.N., Yamamoto, S., 1986. Growth rate and shoot: Root allometry in *Pseudotsuga menziesii* (Mirb.) Franco and *Pinus contorta* Dougl. Seedlings raised under two photoperiodic regimes. *Scand. J. For. Res.* 1, 397–402.
- Burns, R.M., Honkala, B.H., Coordinators, T., 1990. *Silvics of North America: Volume 2. Hardwoods*. U S Dep. Agric. USDA For. Serv. Agric. Handb., 654.
- Ceulemans, R., Mousseau, M., 1994. Tansley review No. 71. Effects of elevated atmospheric CO₂ on woody plants. *New Phytol.* 127, 425–446.
- Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B., Thomas, C.D., 2011. Rapid range shifts of species associated with high levels of climate warming. *Science* 333, 1024–1026.
- Curtis, P.S., Wang, X., 1998. A meta-analysis of elevated CO₂ effects on woody plant mass, form, and physiology. *Oecologia* 113, 299–313.
- Farrar, J.L., 1995. *Trees in Canada*. Canadian Forest Service & Fitzhenry and Whiteside Limited, Markham, Ontario, Canada.
- Gestel, N.C.V., Nesbit, A.D., Gordon, E.P., Green, C., Paré, P.W., Thompson, L., Peffley, E.B., Tissue, D.T., 2005. Continuous light may induce photosynthetic downregulation in onion – consequences for growth and biomass partitioning. *Physiol. Plant* 125, 235–246.
- Hamilton, J.A., Kayal, W.E., Hart, A.T., Runcie, D.E., Arango-Velez, A., Cooke, J.E.K., 2016. The joint influence of photoperiod and temperature during growth cessation and development of dormancy in white spruce (*Picea glauca*). *Tree Physiol.* 36, 1432–1448.
- Hay, R.K.M., 1990. The influence of photoperiod on the dry matter production of grasses and cereals. *New Phytol.* 116, 233–254.
- Heide, O.M., 1974. Growth and dormancy in norway spruce ecotypes (*Picea abies*) I. Interaction of photoperiod and temperature. *Physiol. Plant* 30, 1–12.
- Heide, O.M., Bush, M.G., Evans, L.T., 1985. Interaction of photoperiod and gibberellin on growth and photosynthesis of high-latitude *Poa pratensis*. *Physiol. Plant* 65, 135–145.
- Jackson, S.D., 2009. Plant responses to photoperiod. *New Phytol.* 181, 517–531.
- Johnsen, K.H., Seiler, J.R., 1996. Growth, shoot phenology and physiology of diverse seed sources of black spruce: I. Seedling responses to varied atmospheric CO₂ concentrations and photoperiods. *Tree Physiol.* 16, 367–373.
- Junttila, O., Kaurin, Å., 1990. Environmental control of cold acclimation in *Salix pentandra*. *Scand. J. For. Res.* 5, 195–204.
- Keyes, M.R., Grier, C.C., 1981. Above-and below-ground net production in 40-year-old Douglas-fir stands on low and high productivity sites. *Can. J. For. Res.* 11, 599–605.
- Lambers, H., Chapin, F.S., Pons, T.L., 2008. *Plant Physiological Ecology*. Springer, New York, New York, NY.
- Li, W.-L., Berlyn, G.P., Ashton, P.M.S., 1996. Polyploids and their structural and physiological characteristics relative to water deficit in *Betula papyrifera* (Betulaceae). *Am. J. Bot.* 83, 15–20.
- Li, J., Dang, Q.-L., Man, R., 2015. Photoperiod and nitrogen supply limit the scope of northward migration and seed transfer of black spruce in a future climate associated with doubled atmospheric CO₂ concentration. *Am. J. Plant Sci.* 06, 189–200.
- McGuire, A.D., Melillo, J.M., Joyce, L.A., 1995. The role of nitrogen in the response of forest net primary production to elevated atmospheric carbon dioxide. *Annu. Rev. Ecol. Syst.* 26, 473–503.
- Oleksyn, J., Tjoelker, M.G., Reich, P.B., 1992. Growth and biomass partitioning of populations of European *Pinus sylvestris* L. under simulated 50° and 60° N daylengths: evidence for photoperiodic ecotypes. *New Phytol.* 120, 561–574.
- Pachauri, R.K., Allen, M.R., Barros, V.R., Broome, J., Cramer, W., Christ, R., Church, J.A., Clarke, L., Dahe, Q., Dasgupta, P., 2014. *Climate change 2014: synthesis report. Contribution of Working Groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change*. IPCC.
- Pitelka, L.F., Group, P.M.W., 1997. Plant Migration and Climate Change: A more realistic portrait of plant migration is essential to predicting biological responses to global warming in a world drastically altered by human activity. *Am. Sci.* 85, 464–473.
- Raulo, J., 1976. Development of *Betula pendula* Roth progenies in northern Lapland. *Metsäntutkimuslaitos*.
- Rogers, H.H., Prior, S.A., Runion, G.B., Mitchell, R.J., 1995. Root to shoot ratio of crops as influenced by CO₂. *Plant Soil* 187, 229–248.
- Rogers, H.H., Runion, G.B., Krupa, S.V., 1994. Plant responses to atmospheric CO₂ enrichment with emphasis on roots and the rhizosphere. *Environ. Pollut.* 83, 155–189.
- Saikkonen, K., Taulavuori, K., Hyvönen, T., Gundel, P.E., Hamilton, C.E., Vänninen, I., Nissinen, A., Helander, M., 2012. Climate change-driven species' range shifts filtered by photoperiodism. *Nat. Clim. Change* 2, 239–242.
- Salisbury, F.B., 1981. Responses to Photoperiod. In: Lange, O.L., Nobel, P.S., Osmond, C.B., Ziegler, H. (Eds.), *Physiological Plant Ecology I: Responses to the Physical Environment*. Springer, Berlin Heidelberg, Berlin, Heidelberg, pp. 135–167.
- Saxe, H., Ellsworth, D.S., Heath, J., 1998. Tree and forest functioning in an enriched CO₂ atmosphere. *New Phytol.* 139, 395–436.
- Schreiber, S.G., Ding, C., Hamann, A., Hacke, U.G., Thomas, B.R., Brouard, J.S., 2013. Frost hardiness vs. growth performance in trembling aspen: an experimental test of assisted migration. *J. Appl. Ecol.* 50, 939–949.
- Simard, S., Vyse, A., 1992. *Ecology and management of paper birch and black cottonwood in southern British Columbia*. B.C. Ministry of Forests, Victoria, B.C.
- Stinziano, J.R., Way, D.A., 2017. Autumn photosynthetic decline and growth cessation in seedlings of white spruce are decoupled under warming and photoperiod manipulations. *Plant Cell Environ.* 40, 1296–1316.
- Stulen, I., Den Hertog, J., 1993. Root growth and functioning under atmospheric CO₂ enrichment. *Vegetatio* 104, 99–115.
- Thomas, B., Vince-Prue, D., 1996. *Photoperiodism in plants*. Academic Press.
- Velling, 1979. Initial development of different *Betula pendula* provenances in the seedling nursery and in field trials. *Folia For.* 379, 1–14 In Finnish with English summary.
- Viherä-Aarnio, A., Häkkinen, R., Partanen, J., Luomajoki, A., Koski, V., 2005. Effects of seed origin and sowing time on timing of height growth cessation of *Betula pendula* seedlings. *Tree Physiol.* 25, 101–108.
- Wang, J.R., Hawkins, C.D.B., Letchford, T., 1998. Photosynthesis, water and nitrogen use efficiencies of four paper birch (*Betula papyrifera*) populations grown under different soil moisture and nutrient regimes. *For. Ecol. Manag.* 112, 233–244.