Global warming effects on growth and photosynthesis of northern woody species: silver birch (Betula pendula), Scots pine (Pinus sylvestris) and Norway spruce (Picea abies)

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Abstract

Anthropogenic fossil fuel burning and land use changes are causing increased atmospheric CO₂ concentrations, which lead to global mean temperature elevation. Elevated temperature stimulates the growth of deciduous species in boreal region in general whereas coniferous species may have little ability to respond similarly due to conservative growth strategies. My aim was to investigate the impacts of elevated temperature on the relative changes in growth and photosynthesis in Betula pendula, Pinus sylvestris and Picea abies grown in the same ecosystem. These species are, economically speaking, the most important tree species and having the major distribution in the northern boreal forest. In an outdoor experiment, one-year-old B. pendula and two-year-old coniferous seedlings were grown under ambient and elevated temperature for one growing season. Temperature treatment was given with infrared heaters by increasing the temperature ±2 °C from ambient level. Height and diameter growth was measured every two weeks from May to September and dry shoot biomass was analyzed at the end of the growing season. Chlorophyll content index and gas exchange parameters were observed in July to estimate photosynthesis rate. Elevated temperature significantly increased the height growth (18%) in B. pendula; however, coniferous species were less responsive to temperature. Although statistically not significant, temperature treatment on P. sylvestris showed increased tendency in photosynthesis rate and overall growth performance, especially in needle biomass. On the other hand, P. abies tended to be resistant in response to elevation in temperature. This result implies that, higher temperature will increase the growth of B. pendula and may increase the growth of P. sylvestris seedlings in the boreal region in coming years whereas P. abies may linger with this trend. In the future, experiments which consist of multiple growing seasons with these keystone species would provide more accurate results of overall growth performance.
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1. INTRODUCTION

Boreal forests are located throughout the polar region (45°–70° latitude) of the northern hemisphere which cover 33% of the total circumpolar region (1640 million ha), mainly in the Nordic countries (Finland, Sweden, Norway, Iceland), Russia and North America (Canada, Alaska) (FAO, 2006; 2010). Annual mean temperature of this region varies from -5 °C to +5 °C (Kellomäki, 2016). Boreal forest soils are featured as low nutrient content and water inadequate soil. Flora of boreal forests are dominated by coniferous species; however also mixed with deciduous species especially on fertile sites (Bonan and Shugart, 1989).

In Finland, boreal forests are characterized by small number of tree species where Scots pine (Pinus sylvestris L.) and Norway spruce (Picea abies (L) H. Karst.) are most common coniferous species as well as downy birch (Betula pubescens Ehrh.) and silver birch (Betula pendula Roth) are the most common deciduous species (Kuusela, 1990). According to Kalliola (1973), P. sylvestris distribution ranges from southern (on poor sites) to northern boreal forest whereas P. abies is more dominant in northern part but also grows well on fertile southern sites of Finland. On the other hand, Betula species are commonly distributed with conifers on fertile sites of southern part. Mixtures of all three species are common on fertile to medium fertile sites of northern Europe. According to Finnish Forest Research Institute (2014), P. sylvestris shares 50%, P. abies shares 30% and both Betula share 17% of the total stocking of tree species of Finland’s forest.

Boreal forests of Nordic countries are systematically used for timber and biomass production for decades (Kellomäki, 2016). Resources coming from P. sylvestris, B. pendula and P. abies are the largest contributor to the forest-based bio-economy in northern Europe. All these trees are used for heating, producing electricity, structural materials and many other forest products in Finland. As over 70% of landscape in Finland is covered by forest (FFA, 2014), these tree species have major importance as the habitat for wildlife. Boreal forest acts also as carbon sink, balancing the effect of climate change. Changes in structure of boreal forest would thus have significant effects on the economy as well as ecosystem.
Climate change is defined as any change in climatic variables over time whether caused by natural variables or due to human activities (IPCC, 2013). However, global mean temperature increase due to higher anthropogenic emission is the most related factor of climate change. Global mean annual temperature has already increased by 0.85 °C during the years 1880–2012 especially in last five decades and it is expected to rise even more (0.3 °C – 4.8 °C) by the end of 2100 (IPCC, 2013). However, warming is uneven in the global context since higher latitude would probably experience most evident warming (IPCC, 2013). Finland has already experienced a total increase of 2.3 °C mean annual temperature over the whole country during the period 1847–2013 (Mikkonen et al., 2015), where mean daily temperature has already raised by 0.3 °C per decades after 1960 (Aalto et al., 2016). However, winter temperature increment is likely to be higher than summer temperature increment (Ruosteenoja et al., 2016).

Trees show immediate response to climate change by altering the growth and development within a short term (Kirschbaum, 1999). Increased temperature may facilitate the longer growing season and influence the growth and photosynthesis of the trees positively (Kellomäki and Wang, 2001). Therefore, climatic simulations (process-based simulation model) assume that Nordic coniferous forest stands will have higher net primary productivity because of warming (Bergh et al., 2003). Accordingly, Stinziano and Way (2014) suggested that temperature increment of less than 5 °C may enhance the growth of boreal tree species but higher temperature increment may reduce the growth. Moderate temperature elevation may increase the share of *P. sylvestris* while *P. abies* share may reduce. It has been modelled that under moderate warming, the share of total volume of *P. sylvestris* would be 68%, *P. abies* 12% and *Betula* species 20% over the whole Finland by the year 2099 (Kellomäki et al., 2005). However, estimates are mostly based on greenhouse experiments whereas outdoor conditions may reveal different conclusion because of the interaction of different climatic factors. Thus, impact of elevated temperature on boreal forests is not fully known yet.
2. LITERATURE REVIEW

2.1 Elevated temperature impacts on boreal forest

Although climate change is a global issue, impacts on forests depend on local environmental conditions and management methods (Kellomäki, 2016). For instance, warming has significant effects on boreal forest structure and ecosystems. Numerous studies have already reported that warming climate will increase photosynthesis, and thus enhance biomass growth in broad leaf species under boreal conditions (e.g. Mäenpää et al., 2011; Hartikainen et al., 2012; Lavola et al., 2013). On the other hand, Stinziano and Way (2014) have found that although warming could enhance photosynthetic rates in forests that experience elevated temperatures, it will likely not occur equally in all species. Rather, growth increment would be higher in deciduous species than coniferous species (Way and Oren, 2010).

In a recent meta-analysis, Way and Yamori (2014) found that evergreen woody species, like those that dominate boreal forests, showed the least ability to acclimate photosynthesis to high growth temperatures. However, Ge et al. (2011) has predicted that, elevated temperature on the southern site of Finland would reduce net canopy photosynthesis: -15% in *P. abies*, -12% in *P. sylvestris* and -13% in *Betula* species, respectively, while in the northern site of Finland, warming would increase net canopy photosynthesis 11% in *P. abies*, 21% in *P. sylvestris* and 10% in *Betula* species. Such change in growth and photosynthesis pattern would influence tree species distribution across the boreal forests.

Climate warming is expected to replace boreal forests by temperate forests in the south part of northern hemisphere where boreal forest is still dominant (Soja et al., 2007). This replacement may also cause redistribution of species of the present boreal forests in northern Europe. Falk and Hempelmann (2013) has predicted that, southern areas of northern Europe would have higher dominance of deciduous species; however, coniferous species would remain dominant in the northern areas. In addition, *Betula* species on fertile south sites and *P. sylvestris* in the northern sites of Finland may replace *P. abies* distribution (Kellomäki et al., 2005). On the other hand, elevated temperature is likely to be harmful for the growth of deciduous species grown
near the southern limit of species distribution of the boreal forest because higher temperature would increase the respiration in broad leaves. This would reduce the amount of photosynthates for growth as such was found by Wertin et al. (2011) who has reported growth (height, diameter, biomass accumulation) and photosynthetic reduction but increased respiration in southern red oak (Quercus rubra) due to temperature elevation. Notably, southern red oak is a temperate forest tree species. Indeed, altered species distribution would substantially affect the forest biodiversity. In this respect, proper management of boreal forests is very important to facilitate adaptation to climate change as well as mitigation of harmful effects of climate change. Accordingly, Taeger et al. (2014) have suggested that, if southern provenance of conifer species were replaced by northern provenance in the managed forest, then conifer trees would be more adaptive in changing northern region.

Boreal forests are likely to be vulnerable to climate change due to the prediction of highly pronounced global warming in Northern latitude by 2100 (IPCC, 2013). Olsson (2011) has anticipated that future warming would cause heat stress, drought episodes, and insect-pest outbreaks etc. Thus, increasing global temperature may significantly change the forest structure under boreal condition. Moreover, temperature elevation will interact with other simultaneously changing climatic factors such as increased CO$_2$, altered precipitation pattern, elevated nitrogen deposition etc. which preclude the predictions from single-factor responses. For example, growth increment due to combined effect of elevated temperature and elevated CO$_2$ is higher than alone temperature (Peltola et al., 2002; Kilpeläinen et al., 2005). Elevated CO$_2$ would substantially increase photosynthesis rate in boreal forest (Hyvönen et al., 2007). However, adequate water and nitrogen availability may affect growth increment (Bergh et al., 1999).

Elevated temperature may give longer growing season in higher latitude, but it will also decouple with water deficiency inducing drought stress (Way and Montgomery, 2015). These consequences are already reducing tree growth and increasing tree mortality in boreal region (Peng et al., 2011; Buermann et al., 2013). Moreover, presence of soil water may not enhance the photosynthesis of boreal conifers in dry air (Brooks et al., 1998). In particular in early spring when melted snow increases soil water, it does not affect photosynthesis process due to dry air.
However, higher temperature will enhance the decomposition of organic matters in the soil which will ultimately increase soil nutrient status and thereafter promote growth of trees, but drought stress will remain (Briceño-Elizondo et al., 2006). On the other hand, this increased plant growth will use higher amount of soil nutrient which may ultimately maintain a balance between nutrient supply and uptake. Under proper management conditions (e.g. planting, thinning, rotation length) boreal forest would experience 90% maximum growth increase in the north whereas at most growth in the south may increase up to 20% (Kellomäki et al., 2005; 2008).

While elevated temperature may increase the net primary productivity (NPP) of northern boreal forest (Qian et al., 2010), it should be considered that warming interact with other climatic and environmental variables; this interaction would overestimate the prediction of future growth pattern of boreal forest only due to elevated temperature effect (Kurz et al., 2008). Thus, it is important to understand the warming effect to tree species as well as other factors which may limit the growth response towards climate change.

Higher temperature, water inadequacy, low nutrient content and short-day length, are likely to constrain the ability of boreal forests to respond positively to the warmer climate. For example, moderate temperature elevation would enhance the photosynthesis by stimulating enzyme function, but high heat would cause heat lability of enzymes (Sage and Kubien, 2007; Yamori et al., 2014). Moreover, Stinziano and Way (2014) have identified water as the primary limiting factor of the forest productivity in the future because higher temperature would enhance canopy transpiration. Indeed, combined effect of elevated temperature and water stress would increase plant’s respiration than photosynthesis. Furthermore, short photoperiod may reduce the carbon uptake and productivity of trees despite adequate temperature availability. Stinziano and Way (2014) reported that, photoperiod may limit the phenological responses to elevated temperature in coniferous species in a greater extent than deciduous species.

2.2 Effects of climatic factors on Betula pendula

One of the important tree species of northern latitudes is B. pendula. Economically, it is valuable as a source for the plywood or pulp, paper and board product manufacture via chemical pulping process. Ecologically, it is a food source and host for herbivores, epiphytes and saprophytes.
Elevated temperature has increased overall growth (height, diameter and biomass) and photosynthesis of *B. pendula* in the boreal regions until the optimum temperature is reached in various experiments (Way and Oren, 2010; Mäenpää et al., 2011; Kasurinen et al., 2012; Lavola et al., 2013; Chung et al., 2013; Way and Montgomery, 2015). In fact, elevated temperature increased leaf area and photosynthesis rate which results in higher growth response (Kellomäki and Wang, 2001).

Growth response depends on developmental stage of trees since young seedlings are tended to show immediate response to climate change. In case of *B. pendula*, stem height increment is higher than diameter increment (Kellomäki and Wang, 2001) which may reduce the mechanical strength of the seedlings. However, changes in precipitation even under elevated temperature would have little effect on *B. pendula* (Briceño-Elizondo et al., 2006). Moreover, Lavola et al. (2013) have concluded that, *B. pendula* is quite adaptive and acclimatise to moderate environmental change, which indicates that this species will be able to adapt successfully at northern altitudes in the future.

### 2.3 Effects of climatic factors on *Pinus sylvestris*

*P. sylvestris* is the most frequently distributed tree species in Finnish boreal forest (FFA, 2014). It has greater industrial value for high-quality timber production. Enhanced temperature can boost *P. sylvestris* growth if there is adequate amount of water available (Martinez-Vilalta et al., 2008). Otherwise, high temperatures can increase evaporation rates and affect the growth negatively (Pichler and Oberhuber, 2007). However, Pumpanen et al. (2012) has found that the biomass accumulation in *P. sylvestris* is higher in the warmest (16–22 °C) soil temperature, especially in the below-ground parts of the seedling. Furthermore, elevated temperature has showed positive growth response in *P. sylvestris* in chamber experiment (Peltola et al., 2002; Kilpeläinen et al., 2003; Kilpeläinen et al., 2005).

Similarly, net photosynthesis also increased in *P. sylvestris* seedlings due to warming effects (Kellomäki and Väisänen, 1997; Kivimäenpää et al., 2016). On the other hand, in some experiments warming has shown no influence at all in the growth (Richter et al., 2012).
Kilpeläinen et al. (2005) reported that 14-year old *P. sylvestris* trees had diameter growth which at first was linear, but then levelled off; and height growth which at first (during three years) was exponential, but then turned linear, see also (Kellomäki, 2016, p. 131). Nonetheless, according to species distribution models, there might be a considerable loss of existing *P. sylvestris* in the southern part of northern Europe (Taeger et al., 2014) because the growth of trees does not response to the warming uniformly. For instance, higher temperature is expected to be cautious for the habitat of *P. sylvestris* trees in dry and warm regions, whereas it will increase growth in temperate areas or northern latitudes (Reich and Oleksyn, 2008). Nonetheless, very high temperatures can destruct plant metabolism directly and it should be considered as a serious threat (Rennenberg et al., 2006).

### 2.4 Effects of climatic factors on *Picea abies*

*P. abies* is genetically featured as slow growing species through their evolution and adaptation in boreal forest ecosystem (Kivimäenpää et al., 2017). It produces light-weight wood with high quality fibers, making it an ideal choice in construction and pulping for short fiber in the absence of faster growing species such as eucalyptus. Moreover, it is valued for cultural and traditional purposes. Elevated temperature in southern part of boreal forest is alarming for *P. abies* because warming would reduce its growth (Kellomäki, 2016). In fact, it has been predicted that *P. abies* stands will have considerable habitat loss in Finland and other fast-growing species will replace them (Kellomäki et al., 2008). However, *P. abies* species has shown different responses to higher temperature in aspect of growth. For example, mature *P. abies* growth increased due to warming only when nitrogen fertilization was provided (Sigurdsson et al., 2013).

Negative growth response in *P. abies* seedlings due to elevated temperature was reported by Kivimäenpää et al. (2013; 2017). Furthermore, elevated temperature increased carbon uptake in mature *P. abies* (Hall et al., 2013) whereas photosynthesis was decreased in young seedlings (Kivimäenpää et al., 2013). Virjamo et al. (2014) has found that, shoot growth of *P. abies* young seedlings was unaffected in response to elevated temperature in outdoor conditions but the root: shoot ratio increased in the seedlings. This means that, in early autumn when the plant
shoot growth is completed, it will start to reserve its extra photosynthetic gain as developed due to warming in roots until the late autumn (Puhe, 2003).

2.5 Importance of the study

*B. pendula, P. sylvestris and P. abies* haven’t been studied in detail during their juvenile stage with a monitored and standardised conditions, during the same experimental year. Previously, most of the experiments have been conducted in green house conditions (Kilpeläinen et al., 2005; Pumpanen et al., 2012; Lavola et al., 2013) where plants do not experience natural variations in temperature, light, wind, soil moisture and humidity. Therefore, outdoor study setup is needed to avoid these kinds of problems and to obtain more reliable conclusion. In addition, it is important to observe the warming effect on different species during the same year as the ambient temperature during the growing season vary every year.

Considering all these preconditions, in the present study, over 2000 *B. pendula, P. sylvestris and P. abies* seedlings were exposed to modulated and elevated temperature in an open field to obtain a better understanding of the impact of elevated temperature on these key stone species. It is also worth to mention that our experimental field represents mixed-forest structure since different species were grown in nearby plots.
3. AIM AND HYPOTHESES

The aim of this study was to assess the effects of elevated temperature on the growth performance and gas exchange parameters of one-year-old *B. pendula* and two-year-old *P. sylvestris* and *P. abies* seedlings in an outdoor experiment. Stem height, basal diameter and dry shoot biomass were measured to estimate the growth performance. Furthermore, photosynthesis performance was evaluated by chlorophyll content index (CCI) and gas exchange parameters (assimilation rate, stomatal conductance, transpiration rate and substomatal CO$_2$) measurements.

More precisely, my objective was to assess the following research questions:

a) Does elevated temperature affect the growth and photosynthesis of studied tree species?

b) Does elevated temperature effect on the growth and photosynthesis vary between studied tree species?

For the completion of the work, the following hypotheses were made:

1. Elevated temperature would increase the growth and photosynthesis of *B. pendula* and *P. sylvestris*, but *P. abies* would show reduced trend.

2. Elevated temperature would increase the growth and photosynthesis of *B. pendula* more than *P. sylvestris* and *P. abies*. 
4. MATERIALS AND METHODS

4.1 Experimental field

The experimental field is located at the botanical garden of Joensuu, Eastern Finland (62°35′N, 29°46′E). The field consist of 36 plots in total with the size of 120 cm x 280 cm for each. Before starting the experiment, the plots were cleaned from existing vegetation and filled with 20 cm layer of sand-peat mixture soil. In addition, the experimental field is surrounded by a 1.5 m high fence to protect the plants from the attack of mammal herbivores. Moreover, a metal shelter is set underneath the fence to prevent vole intrusion. Each plot is equipped with adjustable frames. These frames were holding two infrared heaters (CIR110, Frico Partille Sweden), one after another in the middle of the frames in half (18) of the plots (temperature plots, T). At the same time, 18 controlled plots (control, C) are having a wooden piece, which is as same size as IR-heaters in length in order to equalize the shading effect in both treatment and control plots. All the frames were adjusted 60 cm above from the tip of the plants and lifted along seedlings growth. During the growth season, plots were cleaned regularly from the weeds, and the plants were watered to avoid effect of drying.

Figure 1. Picture of the experimental field in summer 2016 (Photo by Virpi Virjamo, PhD).
4.2 Plant material

One-year-old *B. pendula* and two-year-old *P. sylvestris* and *P. abies* seedlings were originated from Tuusniemi nursery, Eastern Finland. All of them are commonly used seedlings for forest plantation. The seedlings were planted in the field on 26th May 2016. There were 48 plants in each plot from the same species but at a random distribution throughout different plots. In total, there was 2160 plants.

4.3 Temperature treatment

There were 18 treatment plots and 18 control plots in total. Among them, six *B. pendula* plots, six *P. sylvestris* plots and six *P. abies* plots were heated. The heating system is a modulated system where temperature is measured from two control plots and ICP program is calculating the wanted temperature (ambient +2 °C). There were total of twelve temperature sensors (pt 1000 thermometers) in the experimental field. Four of them were measuring air temperatures, four of them were measuring soil temperatures, and four of them were controlling the system (Fig. 2).

Among four system control sensors, two were located at control plots and two were located at treatment plots. Data from all sensors were recorded with e-console program. In addition, we adjusted heater height regularly to maintain 60 cm gap from the seedlings top to the heaters. However, in practice +2 °C enhancement was not achieved. In season 2016, the temperature treatment started in late May and ended at end of September. On average, the achieved temperature increment was +1.5 °C although heaters were all time on their maximum capacity during the growing season.
4.4 Height, diameter and biomass measurement

In order to observe the effect of elevated temperature on the studied tree species, stem height and basal diameter of all the experimental plants were measured every second week. For height measurement, longest shoot was measured from the soil level to the tip of the longest shoot (tip of the needles in conifers) by using a measuring stick and basal diameter was measured with an electronic Vernier calliper from 2 cm above the root knot. In total, there was 9 measurements between 31 May and 21 September 2016. Usually the measurement time was in between 8:30am and 12:30pm.
At the end of growing season, 10 plants from each plot were chosen randomly for biomass measurement and cut from the soil level on 28 September 2016. The biomass samples were dried in +60 °C until dryness in paper bags. Leaves or needles and stems of the individual seedlings were weighted separately. Same plants were also sampled for chemical analyses, and weight of those samples was added to total biomass. Also, the number of side branches from the main shoot was counted. Plot averages was used for further calculations (n=6).

4.5 Chlorophyll content index and gas exchange measurement

Chlorophyll content index (CCI for *B. pendula*) and gas exchange measurements (for all species) were done during three sunny days in July. Six plants from each plot were selected randomly which made altogether 72 plants measured for each species. Measurement time was kept between 9am-15pm.

CCI was measured by using CCM-200 chlorophyll meter (Opti-Sciences, Tyngsboro, MA, USA). The instrument calculates CCI with calibrated light emitting diodes (LEDs) and receptors. The LEDs emit specific wavelengths in the red (653 nm) and infrared (931 nm) ranges and the receptors calculate the ratio of transmission of the two wavelengths through a leaf sample which gives CCI, a relative value of the chlorophyll content of leaves and proportionate to the amount of chlorophyll to the sample (similar to Apogee, 2018). While measuring chlorophyll content index, the youngest mature and disease-free leaf having adequate sunlight exposure was selected for measurements. In every sample, there were two measurements considering both left and right side of the leaf and avoiding the central vain. The mean value from these two measurements from same leaf is used for analysis.

The same leaves of *B. pendula* were used for gas exchange measurement and for conifers mature needles from current year growth was used. Gas exchange measurement was including the net assimilation rate of photosynthesis (A), sub-stomatal CO₂ (Ci), stomatal conductance of CO₂ (gₛ) and transpiration rate (E) parameters. These parameters were determined by using a portable photosynthesis system LCpro+ (ADC BioScientific Ltd., Hertfordshire, UK). The LCpro+ is an open-system Infra-Red Gas Analyzer (IRGA) which facilitates ambient fresh air to pass through the plant.
leaf chamber and measures gas exchange of leaves and needles. Calibrations for flow meter and CO$_2$ reference (C$_{ref}$) and CO$_2$ analysis (C$_{an}$) were stabilized before starting the measurement in order to obtain similar CO$_2$ levels ($\Delta$C = 0). The chamber temperature was 25 °C, photosynthetic active radiation (PAR) was 1200 μmol m$^{-2}$s$^{-1}$ and air flow was set at 200 ml/min. The saturating light for the photosynthesis is 1200 μmol m$^{-2}$s$^{-1}$. For developing the light curve, photosynthesis rates were checked at different levels of irradiance i.e. 0, 100, 300, 600, 900, 1200 and 1500 μmol m$^{-2}$s$^{-1}$. In every measurement, the parameter values were recorded after minimum 1.5 minutes of acclimation inside the chamber.

### 4.6 Statistical analysis

In statistical analyses, individuals from same plot are treated as pseudo replicates. The effect of temperature and species on growth and photosynthetic parameters were tested by general linear model using IBM SPSS statistics for Windows (Version 24.0). Temperature and species were used as fixed factor and chlorophyll content index, gas exchange parameters as well as shoot biomass were used as dependent variable.

For height and diameter growth, difference between last and first measurement value was set as dependent variable and first measurement value was set as covariate. Homogeneity of variance (Levene’s test) and normality of residuals of all the variables was checked. To meet assumption of parametric test, height and diameter were square root-transformed, while shoot biomass, CCI, assimilation rate (A) and transpiration rate (E) were log-transformed. Sub-stomatal CO$_2$ (Ci) and stomatal conductance ($g_s$) were examined by Mann-Whitney U and Kruskal-Wallis tests (non-parametric method) for treatment and species, respectively where original data were used without any transformation.
5. RESULTS

5.1 Height growth

*P. sylvestris* and *P. abies* had the active growth period in June, and reached their final height early compared to *B. pendula* that continued to grow until late August (Fig. 3 and 4). There was a statistically significant effect of temperature on stem height (Table 1) of studied plants. At the end of the growing season stem height of *B. pendula* was on average 140.24 ± 2.70 cm, *P. sylvestris* was 42.76 ± 0.60 cm and *P. abies* was 44.79 ± 0.38 cm under treatment condition. Height increment was in average 14.3 ± 3 cm in *B. pendula* under elevated temperature when compared to the control seedlings (Fig. 3). In *P. abies* stem height was showing a reduction tendency under elevated temperature and *P. sylvestris* showed no change between treatment and control plots (Fig. 4). Based on these results, elevated temperature increased 18% more the growth of *B. pendula* compared to that of *P. sylvestris* or *P. abies* (Table 1. Species*temperature interaction).

**Table 1.** F-values and significance of ANOVA obtained from the general linear model analysis for the effects of enhanced temperature, species and their interaction on height, basal diameter and shoot biomass (dry weight) of *B. pendula, P. sylvestris* and *P. abies* (***, P < 0.001; **, P < 0.01; *, P < 0.05;). Height-diameter were square root transformed and shoot biomass was log-transformed to meet normality assumptions.

<table>
<thead>
<tr>
<th>Factor</th>
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<th>Biomass</th>
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<td>Temperature</td>
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<td>Species*Temperature</td>
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Figure 3. Height growth (mean ± SE) of *B. pendula* under control (C) and treatment (T) (n=6).

Figure 4. Height growth (mean ± SE) of *P. abies* and *P. sylvestris* under control (C) and treatment (T) (n=6).
5.2 Diameter growth

Diameter increment was different between species, but elevated temperature had no significant effect and no species-specific response to temperature was recorded (Tables 1, 2). During the last growth measurement (late September), diameter of B. pendula, P. sylvestris and P. abies were on average 9.83 ± 2.7 mm, 6.97 ± 0.6 mm and 6.34 ± 0.38 mm, respectively, in the heated plots. Elevated temperature showed increment tendency in B. pendula (14%) and P. sylvestris (11.9%) compared to control plots related to diameter growth also in late season (Fig. 5 and 6). However, diameter of P. abies showed no difference between heated and ambient plots (Fig. 6). Although not significant, average diameter growth showed higher increment tendency in B. pendula (9-10 mm) when compared to P. sylvestris and P. abies (6-7 mm) (Fig. 5 and 6).

Table 2. P-values obtained from pairwise comparison between species on height, basal diameter and shoot biomass (dry weight) of B. pendula, P. sylvestris and P. abies by using the general linear model analysis. Height-diameter were square root transformed and shoot biomass was log-transformed to meet normality assumptions.

<table>
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<th>Species</th>
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<tr>
<td>B. pendula</td>
<td>0,000</td>
<td>0,000</td>
</tr>
<tr>
<td>P. abies</td>
<td>0,000</td>
<td>0,000</td>
</tr>
<tr>
<td>B. pendula</td>
<td>0,000</td>
<td>0,000</td>
</tr>
<tr>
<td>P. sylvestris</td>
<td>0,000</td>
<td>0,000</td>
</tr>
<tr>
<td>P. abies</td>
<td>0,103</td>
<td>0,047*</td>
</tr>
<tr>
<td>B. pendula</td>
<td>0,000</td>
<td>0,000</td>
</tr>
<tr>
<td>P. abies</td>
<td>0,000</td>
<td>0,000</td>
</tr>
<tr>
<td>P. sylvestris</td>
<td>0,000</td>
<td>0,000</td>
</tr>
</tbody>
</table>
Figure 5. Basal diameter growth (mean ± SE) of *B. pendula* under control (C) and treatment (T).

Figure 6. Basal diameter growth (mean ± SE) of conifers under control (C) and treatment (T).
5.3 Shoot biomass

The variation in shoot biomass accumulation under temperature treatments is presented in Figures 7, 8 and 9. Biomass accumulation was different in all studied species, but temperature showed no species-specific response (Tables 1 and 2). Biomass accumulation was highest in *B. pendula* followed by *P. sylvestris* and *P. abies*. Elevated temperature had a significant effect on leaf biomass accumulation (12.82 ± 0.79 g) in *B. pendula* (Table 1). Compared to control plots, total shoot biomass accumulation showed higher increment tendency in *B. pendula* (26%) and *P. sylvestris* (23.3%) whereas no difference was found for *P. abies*.

![Figure 7](image-url)

**Figure 7.** Total leaf biomass (mean ± SE) of *B. pendula*, *P. Sylvestris* and *P. abies* under control (C) and treatment (T).
Figure 8. Total stem biomass (mean ± SE) of *B. pendula*, *P. sylvestris* and *P. abies* under control (C) and treatment (T).

Figure 9. Total shoot biomass (mean ± SE) of *B. pendula*, *P. sylvestris* and *P. abies* under control (C) and treatment (T).
5.4 Chlorophyll content index (CCI), assimilation rate (A) and transpiration rate (E)

The effect of elevated temperature on the CCI of two-year-old *B. pendula* was statistically significant (Table 4). CCI of *B. pendula* has increased 33% under elevated temperature as compared to the control plots.

All studied photosynthesis parameters differ between studied species (Table 4). *B. pendula* had acquired the highest assimilation rate (29.67 µmol m$^{-2}$s$^{-1}$). There was a significant effect of temperature treatment on assimilation rate (A) (Table 4) indicating that assimilation rate (A) was higher under enhanced temperature when compared to control plants. Under elevated temperature, A was increased 5% in *B. pendula*, 13% in *P. sylvestris* and 20% in *P. abies* as compared to control plots (Table 3). However, interaction between species and the treatment was insignificant.

**Table 3.** *P*-values obtained from pairwise comparison between species on assimilation rate of *B. pendula, P. sylvestris* and *P. abies* by using the general linear model analysis. Assimilation rate was log-transformed to meet normality assumptions.

<table>
<thead>
<tr>
<th>Species</th>
<th>Assimilation rate</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. sylvestris</em></td>
<td>0.000</td>
</tr>
<tr>
<td><em>B. pendula</em></td>
<td></td>
</tr>
<tr>
<td><em>P. abies</em></td>
<td>0.000</td>
</tr>
<tr>
<td><em>B. pendula</em></td>
<td></td>
</tr>
<tr>
<td><em>P. sylvestris</em></td>
<td></td>
</tr>
<tr>
<td><em>P. abies</em></td>
<td>0.000</td>
</tr>
<tr>
<td><em>B. pendula</em></td>
<td></td>
</tr>
<tr>
<td><em>P. abies</em></td>
<td></td>
</tr>
</tbody>
</table>

22
The effects of elevated temperature on transpiration rate (E) was not detected (Table 4). E differs within the species and is equal to 4.78 mmol m⁻²s⁻¹ in *B. pendula*, 0.30 mmol m⁻²s⁻¹ in *P. sylvestris* and 0.18 mmol m⁻²s⁻¹ in *P. abies* was recorded under elevated temperature (Table 4). As a result, *B. pendula* showed increasing tendency (3%) in transpiration followed by *P. sylvestris* and *P. abies*.

5.5 Sub stomatal CO₂ (Ci) and stomatal conductance (gₛ)

The effect of elevated temperature on substomatal CO₂ (Ci) or stomatal conductance (gₛ) was not detected (Table 4). However, both Ci and gₛ was different between species (Table 4). Ci for *B. pendula*, *P. sylvestris* and *P. abies* were 251.22 µmol mol⁻¹, 63.04 µmol mol⁻¹ and 114.43 µmol mol⁻¹, respectively. Furthermore, gₛ for *B. pendula*, *P. sylvestris* and *P. abies* were, 3.87 mol m⁻²s⁻¹, 0.02 mol m⁻²s⁻¹ and 0.01 mol m⁻²s⁻¹, respectively.

Table 4. F-values obtained from the general linear model analysis of the effects of enhanced temperature on CCI, A, and E in *B. pendula*, *P. sylvestris* and *P. abies*. CCI, A and E were log-transformed to meet normality assumptions. Significance of Ci and gₛ were tested with non-parametric tests.

<table>
<thead>
<tr>
<th>Effect</th>
<th>CCI</th>
<th>A</th>
<th>E</th>
<th>Ci</th>
<th>gₛ</th>
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<tr>
<td>Species</td>
<td>---</td>
<td>1920.85***</td>
<td>1934.56***</td>
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<td>Significant</td>
</tr>
<tr>
<td>Temperature</td>
<td>15.1**</td>
<td>6.02*</td>
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<td>Insignificant</td>
</tr>
<tr>
<td>Species*Temperature</td>
<td>---</td>
<td>0.559</td>
<td>0.047</td>
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</tr>
</tbody>
</table>
6. DISCUSSION

6.1 Effects of elevated temperature on *Betula pendula*

In our field experiment, the growth (measured as main-stem height, basal diameter and dry shoot biomass) of *B. pendula* seedlings was responsive to elevated temperature in their first growing season as hypothesized and is similar compared with the earlier literature (Kasurinen et al., 2012; Lavola et al., 2013; Way and Montgomery, 2015). However, it should be also noted that, growth increment highly depends on the developmental stage of seedlings (Kellomäki and Wang, 2001). At juvenile stage, seedlings are more susceptible to environmental change than mature trees (e.g. Kellomäki et al., 2008).

Elevated temperature may influence the growth increment positively in higher latitude because usually optimal thermal growth temperature is not achieved in this region for mainly broadleaved species (Way and Oren, 2010; Chung et al., 2013). Optimum growth temperature for *B. pendula* is approximately 22 °C in Eastern Finland (Kellomäki and Wang, 2001) which is higher than the ambient temperature of our control experimental plots achieved during our experimental season. According to Finnish Meteorological Institute, average summer temperature (May to September) of year 2016 was reported 14.2 °C (May: 12.5 °C, June: 14.4 °C, July: 18.1 °C, August: 15.3 °C, September: 10.6 °C) in Linnunlahti, Joensuu area where our experimental plots were situated. For that reason, it is natural that increase of around 2 °C compared to the ambient temperature would provide more favorable growth conditions. Indeed, elevated temperature stimulated all the measured growth parameters including height, diameter, leaf and stem biomass of *B. pendula*, which is also in line with results from *B. pendula* top-closed chambers experiments (Pumpanen et al., 2012; Lavola et al., 2013). I have observed significant increase in height growth and leaf biomass. On the other hand, basal diameter and stem biomass showed higher increment tendency in *B. pendula* seedlings compared to *P. sylvestris* and *P. abies* under elevated temperature. These phenomena support results of Way and Oren (2010) who have found that stem height growth increment is higher than basal diameter growth increment in response to warming for deciduous species. Furthermore, my results that the biomass
accumulation in *B. pendula* increased at higher temperatures supports Kasurinen et al. (2012) findings.

Increased biomass allocation was closely related to changes in photosynthesis. I observed significant increment of CCI in *B. pendula* under elevated temperature which is consistent with the experiment conducted by Tegelberg et al. (2008). Earlier, empirical studies have demonstrated that similar mode of increment of CCI in deciduous species is common response. For example, Randriamanana et al. (2015) found this increment in European aspen (*Populus tremula*) as well as Li et al. (2011) observed greater CCI in common sea buckthorn (*Hippophae rhamnoides*) as response to warming. Higher CCI may indicate higher photosynthetic assimilate production (Matsumoto et al., 2005). Accordingly, I found significant increase in net assimilation rate in *B. pendula* under elevated temperature. My observation of increased assimilation rate supports the results of Mäenpää et al. (2011) who found that *B. pendula* exhibited higher net carbon assimilation rate through increased leaf area in response to elevated temperature. Lavola et al. (2013) have pointed that *B. pendula* seedlings usually allocate its’ photosynthetic gains particularly to the growth of stem biomass. However, I found higher increment in leaf biomass than stem biomass under treatment condition. Nevertheless, increased CCI is not only factor that influence on photosynthesis increment, but also other physiological factors such as changes in transpiration, stomatal conductance, substomatal CO$_2$ stimulate the overall photosynthesis process under rising temperature. For instance, I observed increment tendency of transpiration (E) (as like Kellomäki and Wang, 2001); and stomatal conductance ($g_s$) but reduction tendency of substomatal CO$_2$ (Ci) in *B. pendula* under warming which may partly explain the reason for significant assimilation rate in treatment plots.

### 6.2 Effects of elevated temperature on *Pinus sylvestris*

In our experiment, *P. sylvestris* seedlings under elevated temperature showed similar height growth to control seedlings. Unaltered height growth under elevation of temperature supports the findings of Taeger et al. (2013) from common-garden experimental field and Pumpanen et al. (2012) from laboratory experiment. On the other hand, increment tendency of *P. sylvestris* in diameter growth (11.9%) and shoot biomass (23.3%) opposed with the results of above
mentioned previous studies. At juvenile stage, elevated temperature has introduced anatomical and biochemical changes in *P. sylvestris* seedlings (Luomala et al., 2003) that can explain also results found here. Also, Way and Oren (2010) conducted that evergreen species are keener to increase diameter growth and leaf biomass rather increasing height growth under warming.

In addition to temperature, water availability is a major climatic driver for the radial growth of *P. sylvestris* (Martínez-Vilalta et al., 2008). Taeger et al. (2013) have suggested that, basal diameter increments of *P. sylvestris* is influenced by soil water availability whereas stem height growth is depending on air humidity. Thus, another causal reason for diameter increment detected here could be the tap root system of *P. sylvestris* which helped the seedlings to acquire soil water. Moreover, the observed higher shoot biomass accumulation tendency, especially needle biomass is consistent with the finding of Kivimäenpää et al. (2017) who suggested that, moderate warming would enhance the size of needle, stem growth and shoot biomass of *P. sylvestris*.

My results partly agree with the findings of Briceño-Elizondo et al. (2006) who suggested that, temperature elevation alone may substantially increase the total growth of *P. sylvestris* because I observed higher photosynthesis tendency in *P. sylvestris* under elevated temperature (as also reported by Peltola et al., 2002, and Kivimäenpää et al., 2016). Kellomäki and Väisänen (1997) has predicted 5% and 25% photosynthesis increment in *P. sylvestris* in the south and north part of boreal forest, respectively, by using process-based ecosystem model. In addition, I found declining drift of substomatal CO$_2$ (Ci) in *P. sylvestris* which might influence the photosynthesis positively as found by Zhao and Liu (2009) for another *Pinus* species. However, in contrast to my findings of assimilation rate increment tendency in *P. sylvestris*, Wang et al. (1995) reported decreased net photosynthesis in the same species, though sapling phase plants, grown in open-top chambers. This photosynthetic reduction happened when the temperature was over 30 °C.

Similarly, increased air temperature did not stimulate photosynthetic carbon gain in *Pinus banksiana* (Jack pine) seedlings mainly due to short photoperiod during autumn season (Busch et al., 2007). Busch et al. (2007), however used large temperature difference between warm autumn (22 °C/18 °C-day/night) and cool autumn (7 °C/5 °C-day/night) with 8 hours
photoperiod which resulted in higher respiration rate than carbon uptake. In practical, this large
temperature difference overestimates the warming prediction. On the other hand, *Pinus
tabulaeformis* (Manchurian red pine) experienced higher photosynthetic accumulation because
of higher foliage pigment production under artificial warming (Zhao and Liu, 2009). Likewise,
elevated temperature has enhanced CCI in chamber grown *P. sylvestris* (Wang et al., 2003).
Therefore, I suggest that moderate warming temperature may accelerate the growth of
*P. sylvestris* when other important environmental factors such as water and nutrient are also
available. In addition, I observed unaltered transpiration (E) and stomatal conductance ($g_s$) under
both treatment and controlled condition but reduced tendency of substomatal CO$_2$ (Ci) in the
treatment plots.

### 6.3 Effects of elevated temperature on *Picea abies*

In our study, warming had no significant effect on overall stem-length, basal-diameter and shoot
biomass of *P. abies* which support previous observations that shoot growth of *P. abies* is not
affected under elevated temperature in outdoor conditions (Slaney et al., 2007; Kostiainen et al.,
2009; Virjamo et al., 2014). In fact, I found reduced growth tendency in *P. abies* seedlings in our
treatment plots (Fig. 9). Similar results have been reported also from mature *P. abies* (Sigurdsson
et al., 2013). In mature trees however, lack of growth increment was suggested to be results of
poor nutrient conditions, whereas here, seedlings were planted on freshly changed soil.

Concerning the growth reduction in *P. abies* growth, Way and Sage (2008) have observed that,
during high temperature exposure (ambient +6 °C) *Picea mariana* develops thermal tolerance
and decreased root: shoot ratio and as a result, seedling became susceptible to soil drying and
less competitive to acquire belowground resources. In contrast, Virjamo et al. (2014) reported
increased root: shoot ratio in *P. abies* seedlings as response to elevated temperature when
seedlings where watered regularly. Likewise, Briceño-Elizondo et al. (2006) found that elevated
temperature slightly increased the growth of *P. abies* tree, but the concurrent reduction of air
moisture reduced the total growth substantially. Thus, even if *P. abies* growth is increased in
future climate, it can also be further affected by low humidity (if drought periods) and nutrient
limitation.
It is noteworthy that, we maintained well-watered and weed controlled optimal growth conditions in our study field which contrasts with natural forest environment. That is why our results should demonstrate best-case scenario of seedlings growth under moderate temperature elevation. Instead, I observed that *P. abies* had reduced height and diameter increment tendency under treatment even though regular irrigation was provided to minimize any drought effect. Similar stem height reduction tendency was reported by Kivimäenpää et al. (2017) and diameter decreasing tendency was found by Kivimäenpää et al. (2013) in *P. abies* seedlings under warming. This result argues with the finding of Barber et al. (2000) and Wilmking et al. (2004) who agreed that, drought was the main causal reason for growth reduction under increasing temperature. Moreover, higher temperature showed declining tendency of shoot biomass of *P. abies* seedlings in our experiment which supports the biomass results of Kivimäenpää et al. (2017).

In this study, air temperature elevation imposed higher photosynthetic tendency in *P. abies* seedlings which is in consistent with Hall et al. (2013) experimental results from mature *P. abies*. In contrast, Kivimäenpää et al. (2013) has reported decreased net photosynthesis in *P. abies* seedlings exposed to moderate temperature elevation. Furthermore, I observed unaltered stomatal conductance (*g*ₚ) which means (according to Kivimäenpää et al., 2017) treatment temperature did not manipulate the gas exchange parameters and transpiration rate of the *P. abies* needles. Considering the increment tendency in assimilation rate, I may assume that, *P. abies* would develop thermal acclimation through higher respiration. Furthermore, higher photosynthesis may stimulate canopy level carbon uptake, nitrogen content as well as biomass production in the future. However, higher respiration in boreal conifers due to warming may limit the carbon sequestration under climatic reconstruction (Stinziano and Way, 2017).

Concerning the growth reduction tendency, I assume that the harmful effects of elevated temperature on *P. abies* growth in our study is probably due to the genetic adaptation of this species into their natural growth habitat (as also reported by Kivimäenpää et al., 2017). *P. abies* seedlings which are adapted to humid, shadier and thus, cooler (than our ambient field temperature) growth environment were stressed because of the exposure of around +2 °C elevated air temperature in the open field condition. In addition, warming enhance the shoot growth initiation and cession in *P. abies* (Slaney et al., 2007). Moreover, *P. abies* seedlings show
predetermined growth trend where seedlings already determined the possible growth of the shoot in the previous growing season (Gyllenstrand et al., 2007).

6.4 Differences between species responses to elevated temperature

Our experimental set-up allowed us to study the elevated temperature effects on three boreal tree species at the same time grown in the same field. This temperature effects on growth depends on whether average treatment temperature was higher or lower than optimum growth temperature (Kellomäki and Wang, 2001). When analyzing the interaction between species and temperature, I found that *B. pendula* have significantly higher vertical growth in response to elevated temperature compared to coniferous species. As broad leaf species *B. pendula* is expected to be benefited by warming in northern latitude (Lavola et al., 2013); however also *P. sylvestris* growth tended to be higher whereas *P. abies* growth was tended to reduce under elevated temperature which supports the modelled growth of these three species by Briceño-Elizondo et al. (2006) and Torssonen et al. (2015).

There was also diameter and shoot biomass increment tendency in *B. pendula* (significant leaf biomass) and *P. sylvestris* but reduced growth tendency of same parameters in *P. abies* with increasing air temperature indicating that *P. abies* were incapable to emulate with *B. pendula* and *P. sylvestris* growth responses under higher growing temperature. In addition, all gas exchange parameters differ between species. I observed, highest net photosynthesis in *B. pendula* followed by *P. sylvestris* and *P. abies*, respectively. However, in our experiment *B. pendula* produced highest growth (increment in height 18%, diameter 14%, and shoot biomass 26%) and assimilation rate than *P. sylvestris* (increment in diameter 11.9% and shoot biomass 23.3%) and *P. abies* (no increment). This may predict that the tree species composition in the boreal zone would change in the future with the higher proportion of *P. sylvestris* occupying the current habitat of *P. abies* as well as increasing distribution of *B. pendula* through acquiring the present sites of *P. sylvestris* (Kellomäki et al., 2008).
*B. pendula* and *P. sylvestris* seedlings are genetically adapted to drier, sunny and warmer growth conditions unlike *P. abies*. Thus, elevated temperature effect on growth of *B. pendula* and *P. sylvestris* were seen as higher growth compared to *P. abies*. In our experiment, temperature sums from average ambient temperature was 1350 degree-days (as calculated based on information of Finnish Meteorological Institute) and from elevated temperature treatment was 1650 degree-days. Temperature sum from elevated temperature treatment for *B. pendula* were falling behind to the species’ optimum value for growth, 2360 degree-days (mentioned in Torssonen et al., 2015). For that reason, elevated temperature increased the growth of *B. pendula* more than the growth of *P. sylvestris* and *P. abies*. Furthermore, temperature sums from elevated temperature treatment for *P. sylvestris* were close to the species’ optimum value for growth, 1445 degree-days (reported in Torssonen et al., 2015) which is why growth of *P. sylvestris* was higher than *P. abies* but lower than *B. pendula* due to temperature effect. Nevertheless, the sums from both ambient and elevated temperature treatments for *P. abies* exceeded the species’ optimum value, 1215 degree-days (mentioned in Torssonen et al., 2015). Thus, elevated temperature showed reduced growth tendency in *P. abies* when compared to *B. pendula* and *P. sylvestris*.

Taken together all these growth and photosynthesis responses of *B. pendula*, *P. sylvestris* and *P. abies* under elevated temperature in our study, we can suggest that, alone warming will prefer the growth phenomena of *B. pendula* and *P. sylvestris* over *P. abies* in future forest regeneration when ample water is available. On the other hand, growth reduction tendency in young *P. abies* seedlings under warming is a signal that, growth is likely to be declined in future also. Under mixed forest condition *P. abies* will in future experience acute competition with broadleaf species during stand establishment (Briceño-Elizondo et al., 2006). Elevated temperature decreases canopy growth and lower shoot biomass in *P. abies* seedlings which will reduce the capability of *P. abies* to accumulate sunlight and below-ground resources even before start competing with deciduous vegetation as predicted by Way and Sage, (2008) for another *Picea* species. In addition, forest pest outbreaks are likely to increase in the northern areas due to climate warming (Parmesan et al., 2005). Furthermore, it is possible that, initial temperature induced growth
response in *B. pendula* and *P. sylvestris* would diminish within few years because enhanced growth would use more nutrient from the soil which ultimately lowers soil nutrient level.

Another prediction is that, higher shoot biomass accumulated from increased growth response will increase the net primary productivity (NPP) of the boreal forest dominated by *B. pendula* and *P. sylvestris*, which will further drive the growing terrestrial carbon sink. Under this circumstance, terrestrial carbon sink will remove anthropogenic emissions which is why changes in climate will slow down (Friedlingstein et al., 2006; Sitch et al., 2008; Peñuelas et al., 2011). Likewise, net primary productivity will (NPP) would influence woody encroachment and thickening particularly in northern hemisphere (Peñuelas et al., 2011).
7. CONCLUSION
This study represents an attempt to investigate how boreal forest tree species will be affected at their juvenile stage in terms of growth and photosynthesis under predicted climatic condition. Obtained results indicate that, *B. pendula* seedlings are more responsive than *P. sylvestris* and *P. abies* to the elevated temperature. Elevation in temperature stimulated the growth performance and net photosynthesis production in *B. pendula*. On the other hand, *P. sylvestris* exhibited growth and assimilates increment tendency whereas *P. abies* was conservative to warming acclimation through increasing growth. I would assume that, in the future deciduous species would be more adaptive to the climatic reconstruction than coniferous species which may induce plant redistribution and habitat loss. However, in the experiment, I was studying elevated temperature effect on young seedlings for one growing season which preclude to predict the effect of same treatment on larger trees or longer growth period. Besides, increasing temperature would combine with different other environmental factors in future such as increasing CO₂, drought stress, nutrient limitation, short photoperiod which may avert such growth increment prediction. Thus, combined effects of climatic variables along with biochemical basis research should be conducted in further studies, which will allow more reliable prediction about plant performance under changing climate.
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