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Growth Responses of Boreal Scots Pine, Norway Spruce and Silver Birch Seedlings to Simulated Climate Warming over Three Growing Seasons in a Controlled Field Experiment

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Abstract: We studied the growth responses of boreal Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* L. Karst.) and silver birch (*Betula pendula* Roth) seedlings to simulated climate warming of an average of 1.3 °C over the growing season in a controlled field experiment in central Finland. We had six replicate plots for elevated and ambient temperature for each tree species. The warming treatment lasted for the conifers for three growing seasons and for the birch two growing seasons. We measured the height and diameter growth of all the seedlings weekly during the growing season. The shoot and root biomass and their ratios were measured annually in one-third of seedlings harvested from each plot in autumn. After two growing seasons, the height, diameter and shoot biomass were 45%, 19% and 41% larger in silver birch seedlings under the warming treatment, but the root biomass was clearly less affected. After three growing seasons, the height, diameter, shoot and root biomass were under a warming treatment 39, 47, 189 and 113% greater in Scots pine, but the root:shoot ratio 29% lower, respectively. The corresponding responses of Norway spruce to warming were clearly smaller (e.g., shoot biomass 46% higher under a warming treatment). As a comparison, the relative response of height growth in silver birch was after two growing seasons equal to that measured in Scots pine after three growing seasons. Based on our findings, especially silver birch seedlings, but also Scots pine seedlings benefitted from warming, which should be taken into account in forest regeneration in the future.

Keywords: boreal zone; climate warming; diameter; forest regeneration; height; root biomass; shoot biomass

1. Introduction

Relatively low species richness and a high proportion of coniferous species is a characteristic feature of boreal zone forests in Northern Europe. For example, in Finland, 80% of the volume of growing stock is represented by Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* L. Karst.), and 17% by birch species (*Betula* spp.) [1]. The growth of boreal tree species is currently limited by a relatively short growing season, low summer temperatures and a limited supply of nutrients [2–4].

Air temperature contributes the most to the timing of growth initiation of boreal tree species in spring and its cessation in autumn [5–7], in conjunction with length of day. However, the growth patterns of different tree species and their responses to changing growing conditions (e.g., climate, site) differ from each other, which also affects their productivity [4]. Height growth of boreal Scots pine and Norway spruce lasts for only a few weeks, because of their predetermined height growth pattern [8,9]. In silver birch (*Betula pendula* Roth), the height growth is mostly free, regardless of age, and its duration is clearly longer than in conifers [10]. Radial growth initiates also a few days later than the height growth, lasting typically until early autumn in all these tree species [11,12]. In the future, climate warming is expected to affect the phenology [7], and growth of trees, for example, [13–21].

Related to global climate change and predicted increases in atmospheric CO_2 concentrations of up to 450–1000 ppm under the Representative Concentration Pathways (range from RCP2.6 to RCP8.5 scenario), the annual mean air temperature and precipitation are projected to increase in Finland by 1.9–5.6 °C and by 6–18%, respectively, by the 2080s compared to the period of 1981–2010 [22]. During the potential growing season (April–September), the mean air temperature is expected to rise by about 1–5 °C and precipitation by 5–11% (range from RCP2.6 to RCP8.5), respectively, compared to the period 1981–2010 [22]. Such changes in the growing conditions are expected to increase the growth especially in silver birch, but also in Scots pine, and possibly decrease it in Norway spruce in boreal conditions, for example, [6,18–21]. Also, biomass growth and its allocation to the above- and belowground parts of trees may be affected under changing growing conditions [19,23,24]. So far, only a few experimental studies exist in which the responses of different tree species (e.g., seedlings) have been studied simultaneously under changing growing conditions, such as temperature elevation, for example, [25]. This is despite the fact that better understanding of growth responses of different tree species to changing growing conditions would provide valuable support for selection of suitable future regeneration material (e.g., tree species and seed origin) for forest regeneration area under a changing climate.

In this study, we investigated the growth responses of boreal Scots pine, Norway spruce and silver birch seedlings to simulated climate warming of an average of 1.3 °C during growing season in a controlled field experiment in central Finland. We had six replicate plots for elevated and ambient temperature for each tree species. The warming treatment lasted for the conifers for three growing seasons (2016–2018) and for the birch two growing seasons (2016–2017). We hypothesized the highest, positive growth responses to the minor warming in silver birch and, to a lesser degree, also in Scots pine, in contrast to Norway spruce seedlings. We also hypothesized that the warming treatment would affect the allocation of biomass to the roots and shoots compared to ambient conditions, and in different ways among tree species. Our simulated warming treatment during a growing season is close to the magnitude of the most optimistic RCP2.6 scenario (i.e., increase of air temperature by about 1 °C, compared to the period 1981–2010), under which climate change mitigation is expected to succeed well [22]. We did not simulate an increase in precipitation along with climate warming, because it is expected to increase only by 5% under the RCP2.6 by the 2080s [22].

2. Materials and Methods

2.1. Experimental Layout and Data Measurements

The experimental field consisted of a total of 36 experimental plots (each 0.80 × 2.40 m, at a distance of 3.0 m from each other) in the Botania Garden, Joensuu, eastern Finland (62°60′ N, 29°73′ E) [26].

In the field, there were six replicate plots for both elevated and ambient temperature for each tree species (Figure 1). The field was surrounded by a 1.5 m high fence, with a metal barrier buried 60 cm into the ground beneath the fence to prevent vole and other mammal incursions.

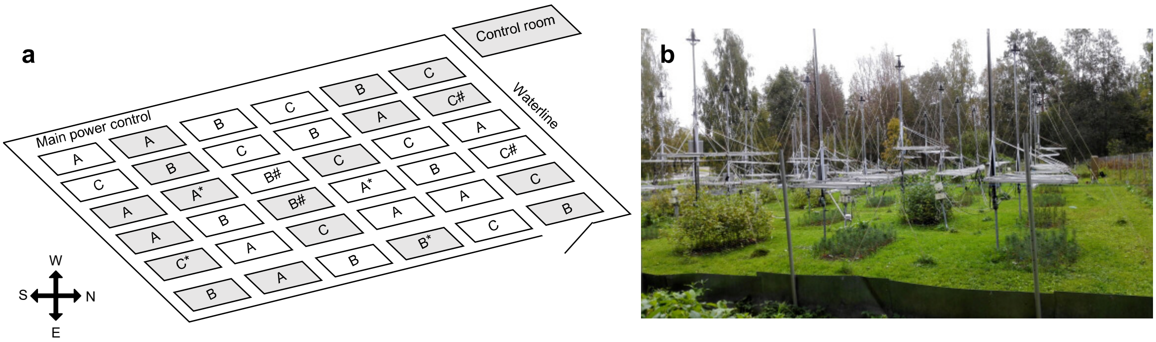

Figure 1. (**a**) Schematic representation of the experimental field. Filled plots (size 0.8 × 2.4 m) represent warming treatment, open plots ambient temperature. A, B and C are *Betula pendula*, *Picea abies* and *Pinus sylvestris*, respectively. # is the air temperature sensor controlling the modulated system, * is equipped with air temperature sensors. (**b**) Photograph of the field seen from the perspective of the control room (photograph by Virpi Virjamo, 2016).

On 26 May 2016, two-year-old Norway spruce seedlings and one-year-old Scots pine and silver birch seedlings were planted in plastic planters (diameter 21 cm, depth 18 cm, volume 4.3 L; TEKU MCL21, Pöppelmann) filled with mineral soil (0.8% limed). The planters were dug into the soil in a single row (north-east side) on each plot at 20 cm intervals (i.e., 12 seedlings per plot, with a total of 144 seedlings per tree species on 12 plots). The seedlings were grown in planters on the experimental field throughout the year. They had contact with surrounding soil only through small holes (for water flow) in the bottom of planters. Seedlings were grown in planters in order to analyze the root:shoot ratios of harvested seedlings in an accurate way.

In other rows of the plots, seedlings (same tree species) not assigned to this study were also planted, but without planters. Additionally, side plants were planted around each plot at 30-cm intervals (19 around each plot, total 684) to prevent edge effects (e.g., drying of the seedlings). All the planted seedlings (seed origins) were from the Saarijärvi nursery (Fin Forelia Oy), which provides forest regeneration materials for practical forestry. Seed origins used in our experiment are suitable for climatic conditions of central Finland.

We simulated on warming plots average temperature increase of +1.3 ± 0.2 °C, compared to the ambient temperature plots, during three consequent growing seasons of 2016–2018. The temperature values were recorded in 10 min intervals. A climate warming was simulated in 18 of 36 plots, using on each plot two infrared heaters of 9.4 cm wide and 125 cm long consecutively (CIR 110, FRICO, Partille, Sweden) (Table 1) situated in the middle of the aluminum frames. On ambient temperature plots, pieces of wood of the same size were situated also in the middle of the aluminum frames, for mimicking the shadowing effect of the heaters and their shadowing effect for rain, respectively. To modulate the system, air temperature was measured from two heated and two ambient plots using PT1000 (Farnell, Helsinki, Finland) probe elements. Four additional plots (three heated and one ambient) were equipped with air temperature sensors, giving a total of eight plots where air temperature was measured (Figure 1a). An ICP100 configuration program (Gantner Instruments, Schruns, Austria) was used to calculate the set point and e-console program for recording the measured data. To ensure the proper functioning of the heaters and the modulated system, checks were performed twice a week.

Table 1. Monthly averages (°C) for the air temperature on control (ambient temperature) and warming (simulated warming of +1.3 ± 0.2 °C) plots, monthly precipitation sum (mm), and temperature sum (T_{sum}, degree days, d.d., with +5 °C threshold) for growing seasons of 2016–2018 in the experimental field, with corresponding 30-year averages (1981–2010) in Joensuu. Comparison to the 30-year averages as percentages are shown in parentheses. [a] Measured 18–31 May, [b] measured 1–6 September.

		Air Temperature °C		
	30-Year Average	**2016**	**2017**	**2018**
Control				
May	8.3		10.1 [a]	
June	14.3	15.0 (105%)	12.8 (90%)	14.4 (101%)
July	16.5	18.6 (113%)	15.8 (96%)	20.2 (122%)
August	14.3	15.7 (110%)	15.6 (109%)	17.1 (120%)
September	8.9	10.8 (121%)	10.8 [b]	
T_{sum}, d.d.		1456	776	1369
Warming				
May			11.3 [a]	
June		16.3 (114%)	14.2 (99%)	15.5 (108%)
July		19.8 (120%)	17.4 (105%)	21.1 (128%)
August		16.9 (118%)	17.1 (120%)	18.1 (127%)
September		12.2 (137%)	12.1 [b]	
T_{sum}, d.d.				
Pine, Spruce		1598	899	1462
Birch		1598	899	1405
		Precipitation mm		
May	31.6	24.5 (78%)	28.9 (91%)	24.3 (77%)
June	56.9	64.1 (113%)	47.6 (84%)	48.3 (85%)
July	66.7	112.4 (169%)	54.8 (82%)	57.7 (87%)
August	73.5	96.5 (131%)	71.7 (98%)	75.8 (103%)
September	56.3	39.0 (69%)	48.0 (85%)	93.9 (167%)

At the beginning of the study, the heaters were set 145 cm from the ground. However, the distance of the frame from the plants was adjusted weekly, if needed, so that the tips of the highest plants were not too close (<60 cm) to the heaters. The heating system was on continuously (24 h per day) from May or June to August or September, depending on the treatment year, giving a total treatment time of three to four months during each growing season (for the warming treatment dates, see Table 2). In 2018, the silver birch seedlings grew so tall that the heating above them needed to be shut off in July for technical reasons (i.e., was in use for only one month).

Table 2. Duration of warming-treatment time periods, growth measurements, and biomass sampling of each growing season of the experiment.

	2016	**2017**	**2018**
Treatment on			
Pine, Spruce	1.6.–29.9.	18.5.–6.9.	31.5.–10.9.
Birch	1.6.–29.9.	18.5.–6.9.	31.5.–2.7.
Weekly measurements			
Height	26.5.–21.9.	15.5.–11.8.	22.5.–29.8.
Diameter	26.5.–21.9.	15.5.–11.8.	22.5.–29.8.
Biomass			
Tree sampling	27.8.	11.8.	4.9.

In the first growing season (2016), the seedlings were watered daily (with water from a nearby lake) during the first week after planting. They were also watered later during the growing season during dry periods, when no rain was obtained for several very warm consecutive days. This was done to enhance the rooting of seedlings in planters. In growing seasons of 2017–2018, watering was not anymore done, despite the occurrence of dry periods. In June 2016, the silver birch seedlings were also treated twice with an herbicide (Baygon aerosol, S. C. Johnson & Son, Inc., Racine, WI, USA), because of unusually large amounts of aphids during the early summer. Weeds within the plots were also regularly removed during all three growing seasons. During the winter of 2016–2017, two pine plots (one ambient and one heated) were severely injured by voles and so they were left out of the study in 2017 and 2018. In addition, seven individuals (three silver birch, two Scots pine and two Norway spruce) in the other plots died or were injured for different reasons during 2017 and 2018.

The height of seedlings was measured each weekday (Monday to Friday) and the stem base diameter three times a week during the growing season, using a digital Vernier caliper (2 cm above the root collar) (Table 2). At the end of each growing season, three to four seedlings from each plot were sampled for their biomass (leaves, needles, branches, stems and roots) measurements (excluding roots in 2017). The seedlings were cut at ground level and dried at 60 °C in a drying room. The roots were washed with water and dried at 60 °C in a hot-air oven. The dried leaves, needles, branches, stems and roots of each individual were weighed separately.

2.2. Data Analyses

The statistical data analyses were conducted on each tree species separately, using IBM® SPSS® Statistics 25 software (Armonk, New York, NY, USA). All the data were tested for normality, and the model fit was evaluated graphically. A linear mixed-effect model was used to test the effects of warming treatment on the height and diameter, and biomass components (shoot, leaves/needles, stem, branches and roots) and the root:shoot ratio of the seedlings harvested at the end of each growing season (Tables S1 and S2). In Norway spruce and Scots pine, the effect of warming treatment on shoot biomass was analyzed for seedlings in all three harvesting years (in 2016, 2017 and 2018), and on root biomass and root:shoot ratio only for seedlings harvested in 2016 and 2018. In silver birch, the effect of warming treatment on the shoot biomass was analyzed for seedlings harvested in 2016 and 2017, and on the root biomass and root:shoot ratio for seedlings harvested in 2016, respectively. Warming treatment was used as the fixed part, and plot as the random part, in the model (Table S1).

A repeated function of the linear mixed-effect model was used for testing the effects of warming treatment on annual height and diameter growth only in those individuals that were harvested at the end of the study period, in 2018. The fixed part of the model included temperature treatment and year, while the random part included the plot. An autocorrelation structure (AR1) was used as a covariance matrix. If there was a significant difference observed for initial values of height and diameter for seedlings between the ambient and warming treatments, they were used as additional covariates in the fixed part of the model. The linear mixed-effect model was used for testing the effect of warming treatment on the duration of 90% of the annual height and diameter growth, and the effective temperature sum (T_{sum} degree days, d.d., with +5 °C threshold) needed for 90% of the mean annual height and diameter growth, respectively. A nonparametric Mann–Whitney test was used when the data were not normally distributed (Table 3). Unfortunately, in 2017, some height and/or diameter growth data needed to be excluded from these analyses for the following reasons. Most of silver birch seedlings did not reach 90% of their total annual height and diameter growth in 2017 until the weekly measurements were stopped on August 11. This was observed also for diameter growth for most of the Norway spruce and Scots pine seedlings in the same year. This was found when comparing initial height and diameter values of seedlings in spring 2018 to their last height and diameter measurements in autumn 2017. In all statistical analyses, if the random-factor parameters for the plot could not be estimated, the plot effect was also left out of the model (Table 3).

Table 3. Results of the linear mixed-effect model and the repeated function of the same model for the effect of the warming treatment and year, and their interaction on different growth parameters in silver birch, Norway spruce and Scots pine seedlings harvested in 2016, 2017 and 2018. The total height and diameter values are given separately for seedlings harvested in different years (2016, 2017 and 2018). The annual height and diameter growth values over years 2016–2018 represent seedlings harvested in 2018. df = degrees of freedom, num df = numerator degrees of freedom, den df = denominator degrees of freedom, *F* = value on the *F* distribution, p = probability of rejecting the null hypothesis.

Variables	Silver Birch				Norway Spruce				Scots Pine			
	Num df	Den df	*F*	*p*	Num df	Den df	*F*	*p*	Num df	Den df	*F*	*p*
Harvested seedlings 2016												
Height total	1	9.883	2.010	0.187	1	10.107	0.261	0.621	1	10	0.077	0.788
Diameter total	1	10	0.135	0.721	1	9.505	0.525	0.486	1	10	0.484	0.502
Shoot biomass	1	10	0.470	0.509	1	46	0.894	0.349	1	10	9.935	0.010
Foliage/Needles biomass	1	10	1.604	0.234	1	46	0.569	0.455 [1]	1	46	12.236	0.001 [1]
Branch biomass	1	10	0.106	0.752	1	46	0.748	0.392 [1]	1	10	0.269	0.615 [3]
Stem biomass	1	10	0.480	0.504	1	46	0.935	0.339 [1]	1	10	2.797	0.125
Root biomass	1	10	0.225	0.645	1	10	0.225	0.645	1	10	3.667	0.085
Root:shoot ratio	1	10	1.516	0.246	1	46	0.111	0.741	1	10	0.235	0.638
Days 90% height				0.000 [2]				0.359 [2]	1	8.299	1.637	0.235
T_{sum} 90% height				0.000 [2]				0.681 [2]	1	8.264	12.655	0.007
Days 90% diameter	1	9.975	0.010	0.921				0.261 [2]				0.065 [2]
T_{sum} 90% diameter	1	10.145	13.180	0.005	1	10.016	19.773	0.001	1	11.758	16.924	0.001
Harvested seedlings 2017												
Height total	1	45	33.673	0.000 [1]	1	8.679	0.089	0.773	1	36	4.469	0.041
Diameter total	1	10	7.263	0.023	1	9.759	2.408	0.153	1	36	62.354	0.000
Shoot biomass	1	10	14.602	0.003	1	46	0.431	0.515	1	7.916	4.960	0.057
Foliage/Needles biomass	1	46	16.884	0.000 [1]	1	46	0.258	0.614 [1]	1	7.989	4.928	0.057 [1,3]
Branch biomass	1	10	2.104	0.178 [3]	1	10	0.083	0.779	1	8.259	1.472	0.259
Stem biomass	1	10	11.637	0.007	1	10	0.005	0.946 [4]	1	7.448	4.397	0.072
Days 90% height								0.004 [2]	1	7.183	0.003	0.961
T_{sum} 90% height								0.381 [2]	1	7.454	8.186	0.023
Harvested seedlings 2018												
Height total					1	10.156	0.339	0.573	1	8.052	17.214	0.003
Diameter total					1	10.622	1.526	0.243	1	8.175	20.270	0.002
Shoot biomass					1	44	11.834	0.001 [3]	1	7.905	14.495	0.005
Foliage/Needles biomass					1	9.940	3.948	0.075	1	7.788	13.292	0.007 [3]
Branch biomass					1	9.990	3.816	0.079	1	8.265	13.576	0.006
Stem biomass					1	9.880	3.491	0.092	1	7.970	1.357	0.005 [3]
Root biomass					1	10.186	2.126	0.175	1	8.125	11.897	0.009
Root:shoot ratio					1	9.756	1.477	0.253	1	8.052	10.923	0.011
Days 90% height								0.936 [2]	1	8.272	3.461	0.099
T_{sum} 90% height								0.151 [2]	1	8.248	0.698	0.427
Days 90% diameter								0.142 [2,5]	1	8.107	1.283	0.290
T_{sum} 90% diameter					1	43	6.597	0.014 [1,6]				0.012 [2]
Annual height growth												
Effect of warming	1	11.074	1.169	0.302	1	9.158	0.035	0.855	1	8.221	21.032	0.002
Effect of year	2	80.803	66.232	0.000	2	82.748	8.910	0.000	2	70.647	11.953	0.000
Year × Warming interaction	2	80.803	14.100	0.000	2	82.748	0.096	0.908	2	70.647	11.824	0.000
Annual Diameter growth												
Effect of warming	1	9.729	1.296	0.282	1	10.703	1.248	0.288	1	8.110	19.373	0.002
Effect of year	2	76.758	146.345	0.000	2	89.432	90.478	0.000	2	66.287	28.148	0.000
Year × Warming interaction	2	76.758	0.571	0.567	2	89.432	2.408	0.096	2	66.287	15.672	0.000

The letter in italics after *p*-value denotes: [1] = plot was not used as a random factor in the model, [2] = a nonparametric Mann-Whitney test was used, transformation made for statistical analyses [3] = ln(x), [4] = ln(K-x), [5] = sqrt(K-x), [6] = 1/x, where K is x_{max} + 1.

3. Results and Discussion

3.1. Evaluation of the Study Approach

We studied in a controlled field experiment simultaneously the growth responses of boreal Scots pine, Norway spruce and silver birch seedlings to simulated minor climate warming (on average of +1.3 ± 0.2 °C), of which magnitude was close to that of the RCP2.6 scenario under the potential growing season (from April to September) by the 2080s [22]. We did not simulate any change in precipitation, because it was expected to increase only by 5% at the same time under the RCP2.6 [22]. There was observed also quite large annual variation in monthly mean air temperatures and precipitation sum values over three consequent growing seasons in 2016–2018 (see Table 1), and as compared to corresponding 30-year averages in the same region (1981–2010). For example, in 2017 June and July were colder and in 2018 July and August were warmer, respectively, than corresponding 30-year averages in the same region (1981–2010). In 2017 and 2018, June and July were also drier (less precipitation) compared to corresponding 30-year averages, and in 2016. Whereas in 2016 June and July were slightly warmer than corresponding 30-year averages and in 2017, respectively. On the other hand, in 2016, June was also slightly warmer and July colder, respectively, compared to 2018. The growing conditions were also presumably even drier on plots under the warming treatment compared to ambient conditions, because of warming of the upper soil layer, too. This was the case especially when the plots were not watered at all during the second and third growing seasons. All these factors may at least partially explain some differences in growth responses of seedlings to the same magnitude of temperature elevation for different tree species over consequent growing seasons.

Originally, the warming treatment was also planned to last for both conifers and birch for three growing seasons. However, due to technical reasons we could run the warming treatment for birch only for two full growing seasons, as they grew too tall on the plots in 2018. In 2017, our weekly growth measurements were finished also two to three weeks earlier (11 August) than in 2016 and 2018, although the warming treatment continued until early September. Despite some limitations of our work, we assume that it will provide a valuable contribution for this research field, where only a few previous experimental studies have correspondingly studied simultaneously the responses of different tree species to temperature elevation (see, e.g., [25]).

3.2. *Growth Responses of Boreal Tree Seedlings to Simulated Climate Warming*

In the first growing season (2016), there were no differences observed in height or diameter growth between the warming and ambient conditions in any of the studied tree species. After two growing seasons (2017), under the warming treatment the total heights of silver birch and Scots pine seedlings were 45% and 11% greater, and their diameters were 19% and 28% greater, compared to ambient conditions (Figure 2, Table 3). After three growing seasons (2018), under the warming treatment, the total height and diameter were, respectively, 39% and 47% greater in Scots pine. However, no difference was detected for them for warming and ambient conditions in Norway spruce either after two or three growing seasons, respectively (Table 3). In Scots pine, warming significantly increased both the annual height and diameter growth in 2017 and 2018. In silver birch, the annual height growth increased significantly by warming in 2017, respectively (Table 3). In our study, the relative height growth response under warming in silver birch was after two growing seasons also equal to that measured in Scots pine after three growing seasons. Also in previous studies, the growth response to warming in deciduous trees has been clearly greater than in coniferous species [13,14].

In our study, the annual diameter growth was in all tree species smallest in 2017 under ambient conditions (Figure 2, Table 3). This result may be at least partially explained by cooler June and July in 2017 and lower precipitation sum during the growing season than in the two other growing seasons (Table 1), which may affect the total annual diameter growth. On the other hand, also weekly growth measurements were stopped two to three weeks earlier (on 11 August) in 2017 than in the other years, which may also partially explain this result (Table 2). However, the annual height growth was in 2017 equal to, or even greater than in 2016 or 2018 for coniferous species (Figure 2, Table 3). The height growth of conifers lasted also only a few weeks since the beginning of the growing season, whereas diameter growth continued until early autumn in all tree species (Figure S1). Thus, shorter measuring period in 2017 did not affect the reported height growth results in coniferous species, unlike in silver birch in which height growth continued for a longer period. A significant interaction between climate treatment and year was found in the diameter and height growth of silver birch and Scots pine.

Also, in previous studies, the growth of Norway spruce (with shallow rooting) has not gained on higher temperatures and it has also suffered from drought [4]. Similar to our study, also in another two-year field experiment for boreal conifers, both the height and diameter of Scots pine seedlings were larger, while the height increment of Norway spruce seedlings was smaller, under an elevated temperature of +1 °C compared to ambient conditions [20]. Also, Kellomäki and Wang [19] reported an increase in height of one-year-old silver birch seedlings under an elevated temperature of +3 °C in a growth chamber experiment. In a chamber experiment under boreal climate in Finland, a temperature rise of 2 °C during the growing season over six years (4 °C in spring and autumn and 6 °C in winter) clearly increased also the height and diameter growth of 20-year-old Scots pine trees [15,16]. Similar increases in growth were not observed in 40-year-old Norway spruce in a three-year climate chamber experiment in Sweden, with a temperature increase of 3.9 °C [17].

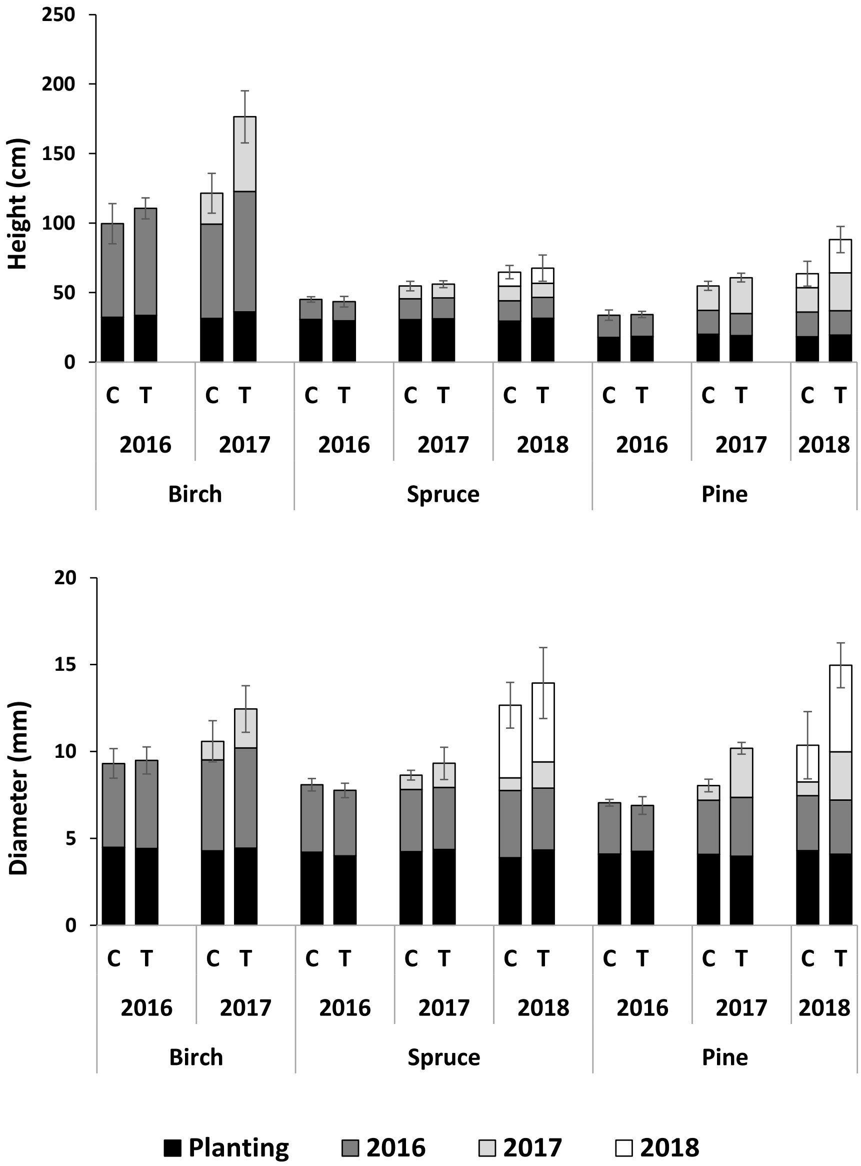

Figure 2. Total height and diameter of silver birch, Norway spruce and Scots pine seedlings harvested in different years (2016, 2017 and 2018) under warming treatment (T) and ambient (C) conditions. The *x*-axes contain the years of harvesting, the colors defining the growth of seedlings in each year before their harvest. The bars represent mean values ± standard deviation (SD).

3.3. Biomass and Root:Shoot Ratios of Seedlings

In 2016, only the shoot biomass of Scots pine increased under warming treatment compared to ambient conditions, being 18% larger. However, the root biomass or the root:shoot ratio was not affected (Table 3). After two growing seasons, the mean shoot biomass was under warming treatment 41% greater in silver birch, but there were no significant differences observed in the coniferous species between warming treatment and ambient conditions (Figure 3, Table 3). After three growing seasons, the mean root and shoot biomass were under warming treatment in Scots pine 113% and 189% greater, and the mean root:shoot ratio 29% lower (Figures 3 and 4, Table 3). At the same time, the mean shoot biomass was 46% greater in Norway spruce under warming treatment.

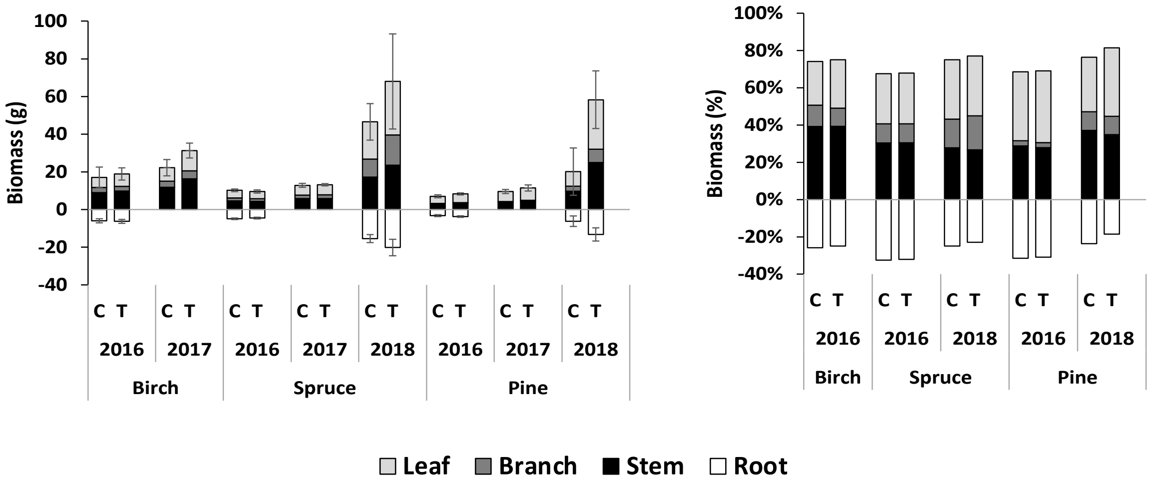

Figure 3. Biomass and its percentage allocation in silver birch, Norway spruce and Scots pine seedlings harvested in different years (2016, 2017 and 2018) under warming treatment (T) and ambient (C) conditions. The *x*-axes contain the years of harvest. Error bars describe the ±SD of shoot biomass and root biomass.

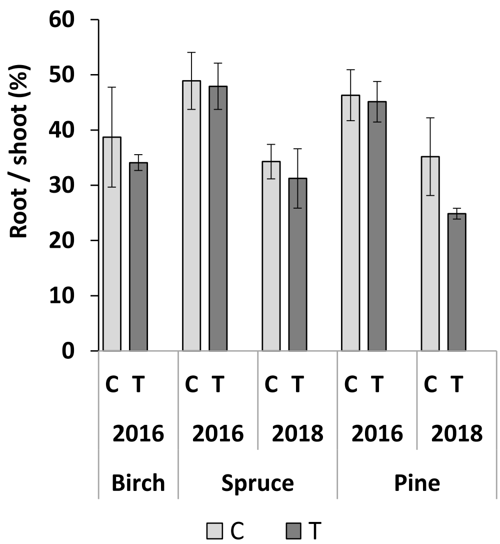

Figure 4. Root:shoot ratio (±SD) in silver birch, Norway spruce and Scots pine seedlings harvested in 2016 and 2018 under warming treatment (T) and ambient (C) conditions. Shoot = above ground mass. The *x*-axes contain the year of plant harvest.

Unexpectedly, only biomass growth of Scots pine seedlings responded positively to the warming treatment during the first growing season. However, the observed shoot biomass response was mainly due to the increased biomass of needles (Figure 3, Table 3). However, after two growing seasons, the shoot biomass of silver birch responded to warming the most. In previous studies, in young boreal tree seedlings, elevated temperatures of 1–3 °C have usually been found to increase the biomass growth in silver birch and Scots pine in different chamber and field experiments, but not in Norway spruce, for example, [18–21]. Also, biomass allocation to the above- and belowground parts of trees have been found to be affected in previous studies under changing growing conditions. A decrease in the root:shoot ratio of one-year-old silver birch seedlings has been observed under 3 °C warming in a growth chamber experiment [19]. Contradictory to our findings, the root:shoot ratio has been shown to increase under elevated temperatures in Norway spruce and in Scots pine seedlings, respectively [23,24]. In our experiment, the planter size (4.3 L) may, however, have restricted the lateral and vertical growth of the roots to some degree, and especially for seedlings grown over three growing seasons in them.

In conifers, a warming of 4 °C in a growth chamber experiment has also increased the aboveground biomass of one-year-old Scots pine and also of two-year-old Norway spruce [27]. In the Sallas et al. [27] experiment, Norway spruce seedlings were NPK-fertilized once a week, but in our experiment they were not. This may have affected the positive growth responses of Norway spruce in Sallas et al. [27]. In an open field experiment of one-year-old Norway spruce seedlings, NPK-fertilization decreased also the root:shoot ratio under warming, as opposed to under ambient temperatures [24].

3.4. Differences in Growth Patterns and Growing Conditions among the Years

Compared to ambient conditions, in the first year under warming treatment, the duration of height growth was, on average, one week longer in silver birch, compared to ambient conditions. In Norway spruce it was, in 2017, three days shorter under warming treatment, respectively (Figure 5, Table 3). The longer duration of height growth in silver birch at least partially explains also its greatest height growth (Figure 2, Table 3). The effective T_{sum} needed for 90% of the annual height growth was also greater under warming treatment than ambient conditions in 2016 in silver birch, and in 2016 and 2017 in Scots pine (Figure 5 and Figure S1, Table 3). The effective T_{sum} needed for 90% of the annual diameter growth was greater under warming treatment in all tree species in 2016, and in Norway spruce and Scots pine in 2018 as well. However, warming treatment did not affect the duration of diameter growth, regardless of tree species (Figure 5 and Figure S1, Table 3).

The positive response in both annual height and diameter growth in Scots pine, and in biomass growth in Norway spruce, were not seen until 2017 and 2018. In Scots pine, the difference in the T_{sum} needed for 90% of the annual height growth between ambient conditions and the warming treatment decreased also considerably from the first year to the third year (Figure 5). The relatively large annual variation in weather conditions during the growing season (Table 1) may have affected this result.

Overall, Scots pine is most tolerant and Norway spruce least tolerant for drier growing conditions among the tree species we studied [4,28]. The future increase in temperature sum during the growing seasons is expected to enhance the growth of silver birch most and that of Norway spruce least, respectively [4,6]. The temperature in the growing season has been found to affect in many previous studies under the current climate the growth of boreal trees clearly more than that of precipitation [11,29–32], as the evaporative demand is low in relation to precipitation [30,33]. On the other hand, precipitation sum from May to July of the previous summer also affects at least the growth in Scots pine for the following year, which may be explained by its predetermined growth pattern (e.g., [29]). Nowadays, the diameter growth lasts typically from mid-May to mid-August in boreal coniferous trees [11,15,34]. About 80% to 90% of it happens also during June and July, and the remaining 5% and 9% in May and August, respectively [11]. Based on it, especially the changes in growing conditions in June and July may affect largely the growth responses of boreal trees also under a warming climate.

In the boreal region, the growing conditions (e.g., temperature sum) are currently also near optimum, especially for Norway spruce, but also partially for Scots pine, unlike for silver birch, which is therefore expected to gain the most from climate change [4]. Due to its mostly free growth pattern, silver birch is also able to gain more for warming and longer growing seasons than Scots pine and Norway spruce with their predetermined growth pattern [4,8–10].

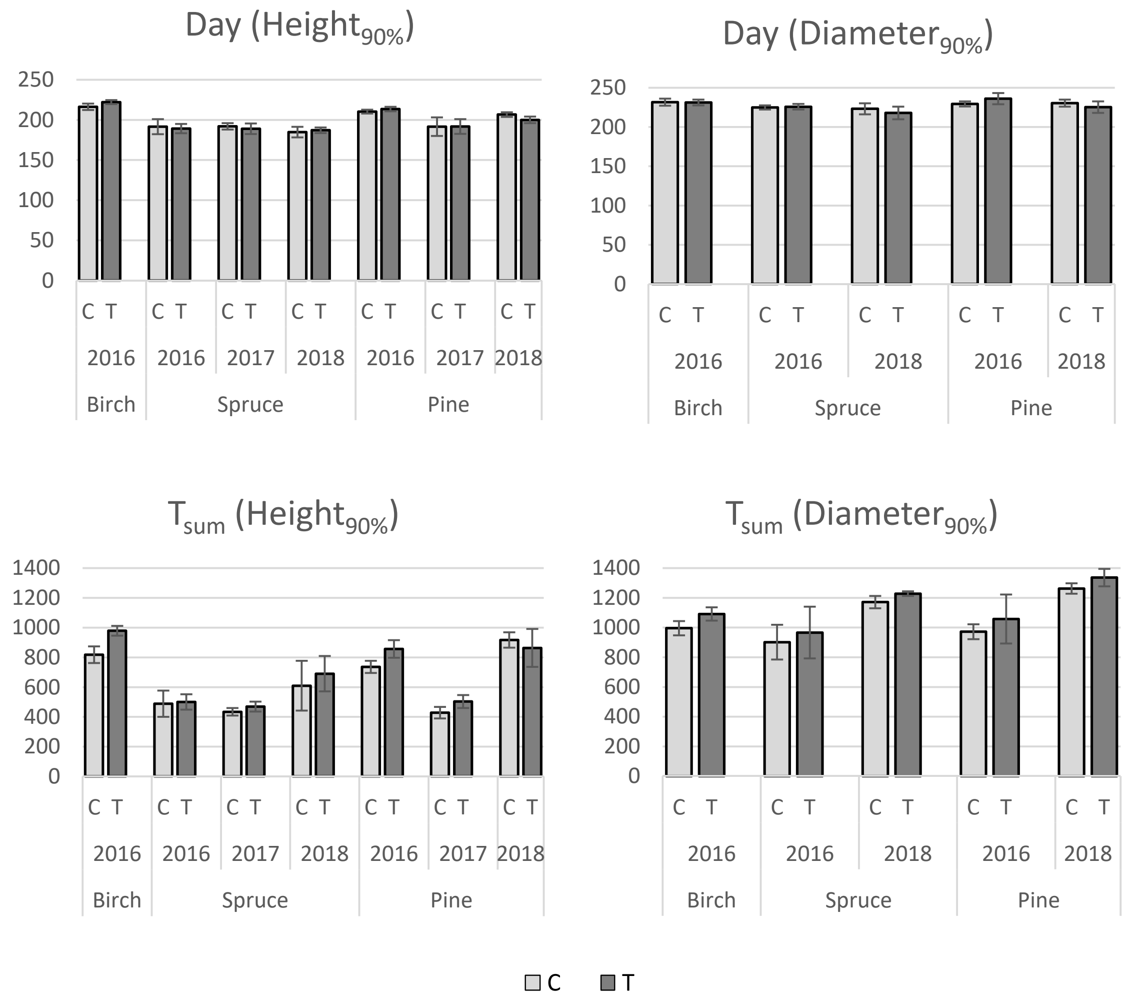

Figure 5. The average day (days from the beginning of the year) (±SD) and average T_{sum} (±SD) on and at which 90% of the annual growth of height (left) and diameter (right) were reached in the silver birch, Norway spruce and Scots pine seedlings harvested in 2018 under warming treatment (T) and ambient (C) conditions.

4. Conclusions

In our study, the seedlings representing main boreal tree species were grown in the same experimental field, sharing equivalent growing conditions, thereby allowing simultaneous comparison of their growth characteristics and responses to simulated minor warming during the consequent growing seasons. Overall, clear differences were observed for growth responses of seedlings for different tree species to warming, as hypothesized. Silver birch and Scots pine seedlings clearly benefitted more from the warming than Norway spruce seedlings, respectively. Some differences in responses of seedlings for these boreal tree species may be related to their differences in growth patterns and biomass allocation to stem, foliage (branches and needles) and roots, respectively. On the other hand, Norway spruce has typically also more shallow rooting, which makes it more prone to drying of the upper soil layer. This was the case in our study especially under warming treatment, without watering during the second and third growing seasons. This may also partially explain the clearly smaller growth response to warming in Norway spruce compared to other tree species. Based on our findings, longer time period than one growing season is needed to study the responses of trees to changing growing conditions. This is because there exists large annual variation in growing conditions between years and some growing seasons may be clearly warmer and drier than others and vice versa, which affects the growth responses of trees, respectively. In future studies, there is also a need to study how changing growth responses of seedlings for these three main boreal tree species under warmer and drier growing conditions will affect the nutrient status of seedlings and consequently also their defensive compound concentrations. This is important as these changes may increase the vulnerability of seedlings to herbivory and decrease their success in forest regeneration. Better growth of birch seedlings under a warming climate will also require timely tending of coniferous stands in order to sustain their growth under a warmer climate.

Supplementary Materials: The following are available online at http://www.mdpi.com/1999-4907/11/9/943/s1, Figure S1: Cumulative growth (%) for each year as a function of the T_{sum} of silver birch, Norway spruce and Scots pine seedlings under warming treatment (T) and ambient (C) conditions. In 2018 the T_{sum} of silver birch seedlings under elevated temperature is lower than in other species, because the warming treatment of silver birch was shorter that year, Table S1: Test variables used in statistical tests of the experiment, Table S2: Number of individuals used in statistical tests of the experiment; (T) warming treatment (C) ambient conditions.

Author Contributions: Conceptualization and methodology, H.P. and R.J.-T.; plant material, T.S.; field measurements and maintenance work, K.N., V.V., L.P., S.K.-a., A.P., N.S., U.S., X.Z. and Z.-M.G.; data analyses, K.N., V.-P.I., A.K. and I.-L.Ä.; writing—original draft preparation, K.N.; writing—review and editing, K.N., H.P., R.J.-T., A.K., V.V., T.S.; visualization, V.-P.I., K.N., V.V.; project administration, resources and funding acquisition, R.J.-T., H.P., K.N. All authors have read and agreed to the published version of the manuscript.

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