Title: Interactive effects of warming and increased precipitation on the physiology, growth, visual condition and soil respiration of Norway spruce seedlings

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Introduction: Studies of boreal tree seedlings suggest that the growth of Norway spruce (*Picea abies*) does not benefit from a warmer climate in the same way as other key species *Pinus sylvestris* and *Betula pendula* in Finland (Kivimäenpää et al. 2017, Pikkarainen et al. 2022). In Finland, the majority of new Norway spruce plantations are established by planting nursery-grown container seedlings from genetically improved seeds produced in seed orchards. A total of 105 million spruce seedlings (60% of all tree seedlings) were delivered for planting in Finland in 2023 (Ruokavirasto 2024). The first few field experiments investigating the impact of warming in Norway spruce used single seedling lots from single nurseries (Riikonen et al. 2012, Kivimäenpää et al. 2017, Pikkarainen et al. 2022). This approach is advantageous in reducing variation due to, for example, the genetic background or nursery management practices, but does not allow generalizations to be made about the warming sensitivity of all Norway spruce seedlings used in forest regeneration. It is also not known how changes in precipitation interact with warming on Norway spruce seedling responses. Both precipitation and drought due to heat events are predicted to increase in northern Europe (IPCC 2024).

Approach: The study was conducted in the new Stress Test Field of the AnaEE Boreal Forest Regeneration (BoFoReg) platform in Suonenjoki, Central Finland. The field allows manipulation of above and below ground temperature and soil moisture in open field conditions with homogeneous forest mineral soil. To improve our understanding of carbon fixation, growth and climate tolerance of Norway spruce seedlings, seedlings from different origins and nurseries were planted in the test field and exposed to three temperature and two soil watering treatments alone and in combination.

Main body of the abstract: Eleven lots of one-year-old Norway spruce seedlings were obtained from four commercial tree seedling nurseries. All the lots were grown using genetically improved first-generation seed orchard seeds. The freezer-stored seedlings were thawed and planted in 24 plots of the Stress Test Field in early June 2023. Plot soils consisted of fine moraine consisting of ≥ 30% mineral soil of Ø <0.06 mm and ≥ 5% mineral soil of Ø <0.002 mm. Each plot had 88 experimental seedlings (8 for each seedling lot). In the Stress Test Field, canopy warming was provided by infrared heaters and below-ground warming by buried resistance heating cables. Target warming treatments were: ambient temperature, +2 °C and +5 °C. Heating systems were tested beforehand under the field and laboratory conditions. Half of the plots in each warming treatment received ambient precipitation and the other half received watering through a subsurface drip irrigation system. The six treatments were divided into four blocks. Heating and irrigation were stopped at the end of the growing season (early October). Seedlings were under natural snow cover until mid April 2024.

Five seedling lots were selected for plant physiological measurements. Net photosynthesis and stomatal conductance were measured (Licor 6400 XT) once a month in July and August, and chlorophyll fluorescence Fv/Fm (Walz MiniPAM) in July-September and also after snowmelt in April 2024. Soil respiration was measured in July, August and September (Licor 6400 XT). All seedling lots were assessed for lammas growth and insect damage late summer and for height and basal stem diameter growth at the end of the growing season. After winter, the visual condition (missing or damaged needles, seedling death, needle color) of the seedlings was assessed, and the growth potential of the new shoots was determined by placing detached shoot tops in water and observing bud opening in the laboratory. Binary data were analysed using GLIMMIX (SAS) and continuous data using Genlinmixed (SPSS), with temperature, watering and seedling lot as fixed factors, and block and plot nested within block as random factors.

The difference in soil temperature at a depth of 15 cm between ambient and target +2 °C was on average 2.4 °C during the day and 2.6 °C at night. The differences between ambient and target +5 °C were 5.5 °C and 6.1 °C respectively. Needle surface temperatures were monitored with a thermal camera. Due to the wind, the temperature increase remained below the targets, about 1 °C at the target +2 °C and 1.3 - 2.0 °C at the target +5 °C. Natural precipitation in the 2023 growing season exceeded long-term averages. On average, supplemental irrigation increased soil moisture by 4% at ambient temperature and 11% at target +2 °C, but no increase was observed at target +5 °C.

In July, stomatal conductance was increased by target +5 °C treatments compared to lower temperatures with ambient precipitation. Net photosynthesis was not affected by the treatments. In July, warming treatments increased Fv/Fm. In August the increasing effect of +2 °C warming on Fv/Fm was still detected in ambient precipitation. In April, after snowmelt, Fv/Fm was reduced by increased watering. Soil respiration was increased by warming in August and September. Soil respiration was also reduced by increased watering in September.

Warming treatments doubled the risk of lammas growth, with different probabilities of occurrence in the seedling lots. Increased growth in the warming treatments (main shoot length and basal stem diameter in 2023) was observed in five of the eleven seedling lots at ambient precipitation. One of the lots benefited from a target warming of +2 °C only. The remaining six lots were unaffected by warming. The increases in the growth of the affected seedlings could not be explained by the lammas growth. The growth responses of the seedling lots to watering were variable, with two benefiting, two suffering and seven unaffected by the watering treatment.

Visible symptoms of drought, fungal disease or insect damage were mild and mortality at the end of the growing season was very low, and no treatment effect was observed. However, after winter watering treatments reduced the probability of healthy-looking seedlings: the average was 90 % for ambient precipitation and 85% for watering. After winter, needles were greener in the warming treatments and more yellow in the watering treatments. The growth potential of new shoots after winter was reduced by watering treatment at ambient temperature. There were also differences in condition and Fv/Fm between seedling lots after winter. Some of these differences could be related to seedling performance during the growing season. For example, a seedling lot with the lowest net photosynthesis and stomatal conductance in the previous summer had the worst shoot condition and lowest Fv/Fm after winter. In addition, a seedling lot with the highest risk of insect damage during the growing season had the most yellow needles after winter.

Conclusions: Watering treatment in rainy summer caused negative effects on seedling vitality. Growth of Norway spruce seedlings can benefit from warming, but not with the tested increase in precipitation. Increased precipitation during the growing season can reduce the field success of Norway spruce seedlings in the next season, as seen here in poorer seedling condition, reduced bud break, more yellow needles indicating lower chlorophyll concentration, and lower Fv/Fm indicating problems with photosystem II function in spring. However, warming improved seedling vitality after winter and may ameliorate some of the negative effects of increased precipitation. Increased lammas growth due to warming can make new shoots more susceptible to autumn frosts, but here thick snow cover protected the seedlings. Increased soil respiration is a factor that reduces the carbon balance of young spruce plantations in a warmer climate. It is noteworthy that warming only increased the growth of some of the seedling lots, and the response of seedling lots to watering treatment also differed.

Learning Objectives: Our results of early field success of Norway spruce seedlings suggest that spruce seedlings may not be as sensitive to climate change than earlier thought. To know the success of a tree species in a changing climate, experiments should include more variable seedling material and consider the influence of genetic background and nursery management practices. The effects of warming and watering treatment had opposite effects on seedling performance, and more studies are needed on the interaction of changes in precipitation and warming. Automatic rain covers will be taken in use in 2025 for better control of precipitation. The water balance of the field has been improved by ditching in 2024. This study focused on early field success of Norway spruce seedlings and was the first experiment where the Stress Test Field was used. The future studies using the Stress Test Field will also span longer than one growing season.

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