

Tree fine root longevity and effects of soil waterlogging, a constraining environmental factor

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Introduction

In forest ecosystems, fine roots play a significant role in carbon (C) and nutrient cycling and allocation, since up to 75 % of the carbohydrates produced by forest trees can be allocated below ground for growth and maintenance of fine roots (Keyes and Grier 1981; Vogt et al. 1996; Helmisaari et al. 2002), which roots are one of the main factors affecting the soil C pool (Clemmensen et al. 2013, Kriiska et al. 2019). This is of special importance, as boreal forests account for approx. 50% of the world's forest ecosystem C (DeLuca & Boisvenue 2012). Root-derived inputs, e.g., through decomposing litter and root exudates, represent a significant C flux in forest ecosystems (Silver & Miya 2001) and a major C flow into the soil (Leppälampi-Kujansuu et al. 2014, Kögel-Knabner 2017).

For getting an overall picture of plant roots and their effects on soil C sequestration and C cycling in a changing climate, it is very important to know the longevity and annual turnover of roots and how these are affected by environmental factors. Future climate scenarios for the boreal zone project increasing temperatures and precipitation, as well as extreme weather events such as heavy rain during the growing season (Kreuzwieser & Gessler 2010, IPCC 2023). This can result in more frequent short-term waterlogging (WL) leading to unfavourable conditions for tree roots. For the future management and sustainable use of boreal forests, it is crucial considering the tree responses to an elevated soil water table and the concurrent oxygen limitations, especially in peatlands. In addition, there are indications that root-derived C is much likelier to contribute to long-term soil C than aboveground plant C (Sokol et al. 2019). Due to the laboriousness and difficulty of the work and methodology related to plant roots, observations on root growth, dynamics and longevities are scarce. This results in scarce data of root traits and limited understanding of their relationship with soil properties and, consequently, that soil C models are focused more on aboveground plant parts. Annual fine root turnover is difficult to estimate as production and death occur at the same time and place. One alternative for studying and following the growth of tree roots are minirhizotrons (Cheng et al. 1991, Johnson et al. 2001).

Approach

The Joensuu Root Laboratory (aka dasotrons) is a unique research facility for studying the effects of environmental conditions on above- and belowground plant processes under controlled conditions, especially in the context of climate change. The experiments conducted in the Joensuu dasotrons include a large variety of plant morphological, anatomical, physiological, and phenological measurements. In a broader context, the general framework of studies in the Joensuu Root Laboratory are linked to plant acclimatisation and adaptation to varying and changing weather and climate conditions, effects of environmental conditions on plant growth and production, and C and nutrient cycles of trees and forests. The research facility allows studying mechanisms connected with responses of root and shoot growth, allocation patterns and C sequestration to changing environmental factors. The special feature of the facility is that air and soil temperatures can be controlled independently from each other (soil temperature below 0 degrees), and that the annual plant cycle can be accelerated. This allows a faster realisation of experiments, that specifically aim at assessing plant mechanisms, and how they are affected by environmental conditions. One advantage of the facility is that all kind of plants can be studied, like cereals, pasture plants, perennials or tree seedlings and saplings. Using a minirhizotron camera, we can study root growth and how it is affected by environmental factors. The root research team at Luke Joensuu has long experience of conducting experiments, and the facility has been used for extensive studies into about the effects of extreme conditions on boreal forest tree seedlings, e.g. low soil temperature, soil frost conditions, WL during the dormancy or growing season, or soil drought conditions. These environmental factors will have an increased importance in a changing climate, and in this respect the Joensuu dasotrons offer a valuable research platform.

For studying constraining effects of adverse soil conditions (here soil WL) on tree fine root survival, results from four different experiments were combined in this work (Roitto et al. 2019, Domisch et al. 2020, Repo et al. 2020, Repo et al. 2021). They differed in duration and tree species, but they had a common treatment (WL) with different timing and duration. All treatments comprised also a control (CTRL) treatment without any constraining factor. Using this approach, we can compare different treatments withing the same tree species, or different tree species with a similar treatment. All experiments assessed the effects of WL of different timing and length, three of them with Scots pine (*Pinus sylvestris* L.) and one with silver birch (*Betula pendula* Roth.). We conducted survival analyses of short (i.e. first order) roots from the minirhizotron images, using the time frames of individual short roots from appearance to disappearance as previously identified and analysed (more details in the respective publications). We used the 'interval' package in R, and survival

analyses with right censored data for assessing differences, either between different types of WL (treatment data) or between tree species (CTRL data).

Results and Discussion

Our results showed that birch roots had a significantly shorter lifespan than pine roots, as the estimations for median survival time, when 50% of the respective roots still are alive, were clearly lower for birch than for pine both in the CTRL and WL treatments (Figures 1–2, Tables 1–2). This is in accordance with previous studies indicating shorter longevities of roots of deciduous trees compared to conifers. (e.g. Hansson et al. 2013, Huang et al. 2024).

Waterlogged soil conditions during the dormant season did not have any clear effects on root survival, whereas WL significantly decreased the median survival times when the WL treatment occurred during the growing season (Figs. 1 and 2). The longer the WL conditions lasted, the more detrimental effects were observed. Thus, elevated water tables during the growing season can have severe effects on the fine roots of Scots pine. This obviously depends on the duration of the exposure and can lead to decreases in C assimilation and allocation to the roots (Repo et al. 2016, Domisch et al. 2020).

Table 1. Statistical results of Kaplan-Meier estimated survival analyses (asymptotic logrank test) of pine and birch short roots in CTRL and soil waterlogging (WL) treatments of different timing and duration in four experiments (total length of experiments are shown). D: waterlogging treatments during plant dormancy, GS: waterlogging during growing season. The number of weeks refers to the duration of the waterlogging treatment. Positive score statistics imply earlier failures than expected (shown in bold).

Experiment	CTRL		WL		Length of experiment days
	Score Statistic	N	Score Statistic	N	
PINE_D_6 weeks	-78.8	1354	-47.0	1168	248
BIRCH_D_6 weeks	390.5	1238	158.9	1423	222
PINE_GS_5 weeks	-200.9	507	-82.0	520	369
PINE_GS_2 weeks	-110.7	1639	-29.9	3472	378
Chi Square	1034.6		156.7		
P-value	<0.001		<0.001		

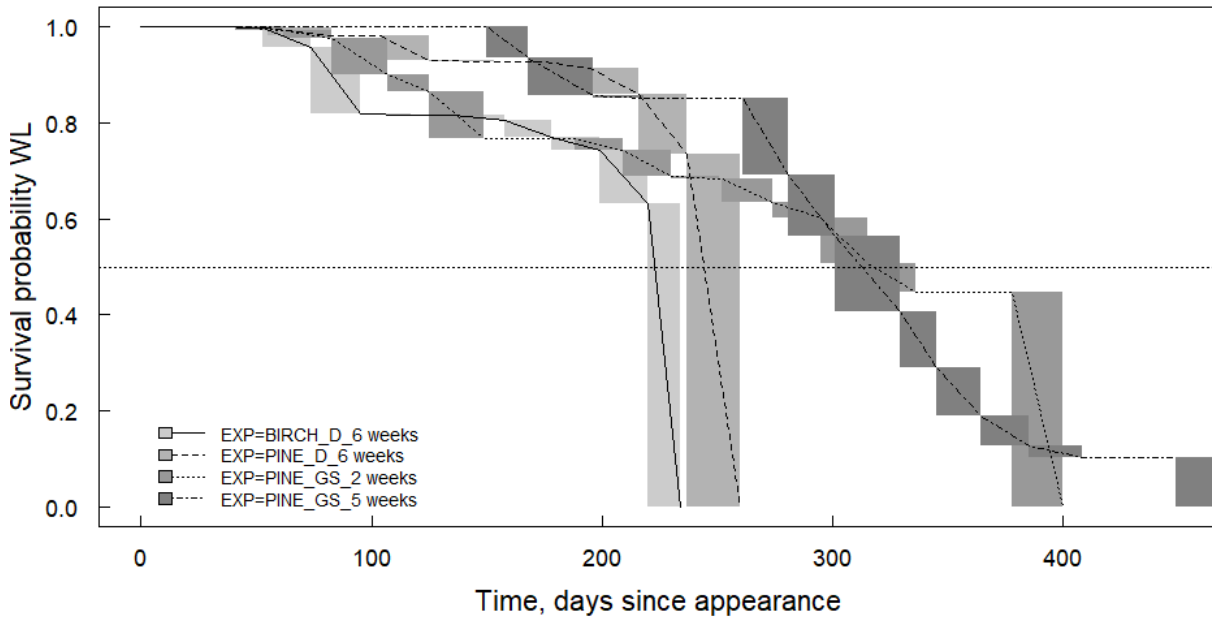


Figure 1. Kaplan-Meier estimated survival probabilities of pine and birch short roots in waterlogging (WL) treatments of different timing and duration in four experiments. D: waterlogging treatments during plant dormancy, GS: waterlogging during growing season. The number of weeks refers to the duration of the waterlogging treatment. The dashed vertical line depicts the median survival time.

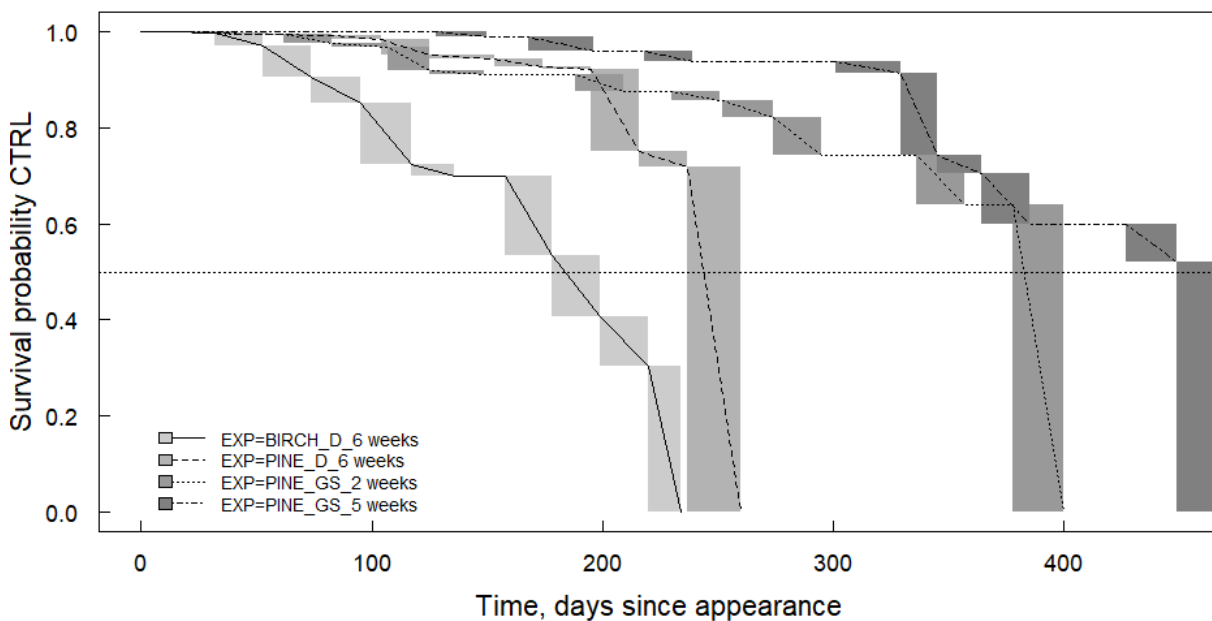


Figure 2. Kaplan-Meier estimated survival probabilities of pine and birch short roots in CTRL treatments in four experiments. The dashed vertical line depicts the median survival time.

Table 2. Median survival times (days) of pine and birch short roots in CTRL and water logging (WL) treatments of different timing and duration in four experiments. D: waterlogging treatments during plant dormancy, GS: waterlogging during growing season. The number of weeks refers to the duration of the waterlogging treatment. Lower and upper limits of 0.95% confidence and numbers of observation (N) are also shown (NA = not applicable, in cases when survival curves did not reach 0.5).

Experiment	CTRL			WL		
	Median, days	0.95 CL	N	Median, days	0.95 CL	N
BIRCH_D_6 weeks	188	126 – NA	1238	227	210 – NA	1423
PINE_D_6 weeks	248	226 – NA	1354	248	NA – NA	1168
PINE_GS_5 weeks	NA	354 – NA	507	315	271 – 354	520
PINE_GS_2 weeks	389	346 – NA	1639	326	263 – NA	3472

Conclusions

By combining results from different experiments conducted in the Root Laboratory, we can provide new information for a better understanding of processes. Here we showed effects of soil waterlogging of different timing and duration by combining data of four experiments.

Our data clearly shows adverse effects of soil waterlogging on tree root growth. Because of the high importance of fine roots for tree growth and C sequestration in forest ecosystems, their responses to elevated water tables should be considered in sustainable use and management of boreal peatland forests, for example, by continuous cover forestry and (or) ditch network maintenance.

Learning objectives

The Joensuu Root Laboratory platform can be used for a large variety of experiments for assessing effects of environmental factors on plant growth, physiological traits, acclimation, and survival. Also, data from previous experiments can be used for obtaining new information when field data are scarce. On the other hand, data from laboratory experiments should be validated under field conditions but laboratory experiments can contribute to a better understanding of mechanisms as such and can improve models in absence of real-world data.

References

- Cheng W et al. (1991) Measuring root turnover using the minirhizotron technique. *Agric Ecosyst Environ* 34: 261–267
- Clemmensen KE et al. (2013) Roots and Associated Fungi Drive Long-Term Carbon Sequestration in Boreal Forest. *Science* 339:1615–1618, doi:10.1126/science.1231923
- DeLuca TH & Boisvenue C (2012) Boreal forest soil carbon: distribution, function and modelling. *Forestry* 85:161–184, doi:10.1093/forestry/cps003
- Domisch T et al. (2020) Here comes the flood! Stress effects of continuous and interval waterlogging periods during the growing season on Scots pine saplings. *Tree Physiol* 40: 869–885, doi: 10.1093/treephys/tpaa036
- Hansson K et al. (2013) Fine root production and turnover of tree and understorey vegetation in Scots pine, silver birch and Norway spruce stands in SW Sweden. *For Ecol Manage* 309: 58–65, doi: 10.1016/j.foreco.2013.01.022
- Helmisaari H et al. (2002) Below- and above-ground biomass, production and nitrogen use in Scots pine stands in eastern Finland. *For Ecol Manage* 165: 317–326, doi: 10.1016/S0378-1127(01)00648-X
- Huang X et al. (2024) Evolution history dominantly regulates fine root lifespan in tree species across the world. *For Ecosyst* 11: 100211, doi: 10.1016/j.fecs.2024.100211
- IPCC (2023) *Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* (Core Writing Team, H. Lee and J. Romero (eds.)). IPCC, Geneva, Switzerland, doi: 10.59327/IPCC/AR6-9789291691647
- Johnson MG et al. (2001) Advancing fine root research with minirhizotrons. *Env Exp Bot* 45: 263–289, doi: 10.1016/S0098-8472(01)00077-6
- Keyes MR and Grier CC (1981) Above- and belowground net production in 40-year-old Douglas-fir stands on low and high productivity sites. *Can J For Res* 11: 599–605, doi: 10.1139/x81-082
- Kreuzwieser J, Gessler A (2010) Global climate change and tree nutrition: influence of water availability. *Tree Physiol* 30:1221–1234, doi: 10.1093/treephys/tpq055
- Kriiska K et al. (2019) Variation in annual carbon fluxes affecting the SOC pool in hemiboreal coniferous forests in Estonia. *For Ecol Manage* 433:419–430, doi:10.1016/j.foreco.2018.11.026

- Kögel-Knabner I (2017) The macromolecular organic composition of plant and microbial residues as inputs to soil organic matter: Fourteen years on. *Soil Biol Biochem* 105: A3–A8, doi:10.1016/j.soilbio.2016.08.011
- Leppälampi-Kujansuu J et al. (2014) Fine root longevity and carbon input into soil from below- and aboveground litter in climatically contrasting forests. *For Ecol Manage* 326: 79–90, doi:10.1016/j.foreco.2014.03.039
- Repo T et al. (2020) Dynamics of fine-root production and mortality of Scots pine in waterlogged peat soil during the growing season. *Can J For Res* 50: 510–18, doi: 10.1139/cjfr-2019-0163
- Repo T et al. (2021) Dynamics of above- and belowground responses of silver birch saplings and soil gases to soil freezing and waterlogging during dormancy. *Tree Physiol* 41: 1143–1160, doi: 10.1093/treephys/tpab002
- Roitto M et al. (2019) Waterlogging and soil freezing during dormancy affected root and shoot phenology and growth of Scots pine saplings. *Tree Physiol* 39: 805–818, doi: 10.1093/treephys/tpz003
- Vogt KA et al. (1996) Production, turnover and nutritional dynamics of above- and belowground detritus of world forests. *Adv Ecol Res* 15: 303–307, doi: 10.1016/S0065-2504(08)60122-1