

# FORHOT-FOREST

## Final Report – 1.2 Research Overview



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November 2019

# ICELANDIC RESEARCH FUND

This final report covers the whole grant period 01.06.2016 - 30.06.2019.

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## Signatures

This is to certify that all information in the annual report is correct and that the report includes all relevant information.

Date and place Keldnaholt, Reykjavík, 15.12.2019
Principal investigator 
Person responsible for research facilities  Ragnheiður I. Þórarinsdóttir (rector)

## Table of Contents

<b>1. ForHot's experimental setup: short overview</b> .....	5
<b>2. The original research plan</b> .....	6
<b>3. The time plan of ForHot-Forest</b> .....	7
<b>4. The modified research plan for the ForHot Forest PhD study</b> .....	8
<b>5. Primary publications and other products from ForHot</b> .....	10
<b>6. The research outputs / state of knowledge</b> .....	14
<b>6.1 Monitoring of environmental drivers</b> .....	14
<i>6.1.1 Soil temperature</i> .....	14
<i>6.1.2 Soil water availability</i> .....	15
<i>6.1.3 Other variables</i> .....	16
<b>6.2 WP I: Tree growth and production response</b> .....	17
<i>6.2.1 Forest production (C-stock changes)</i> .....	17
<i>6.2.2 Radial growth and height growth phenology</i> .....	19
<i>6.2.3 Leaf Area Index</i> .....	23
<i>6.2.4 Fine root biomass</i> .....	23
<b>6.3 WP II: Plant carbon fluxes</b> .....	24
<i>6.3.1 Litter fall</i> .....	24
<i>6.3.2 Fine root turnover and production</i> .....	24
<i>6.3.3 Photosynthesis</i> .....	27
<i>6.3.4 Respiration</i> .....	28
<i>6.3.5 Other measurements</i> .....	29
<b>6.4 WP III - Ecosystem C-balance</b> .....	31
<i>6.4.1. Soil respiration</i> .....	31
<i>6.4.2. Other Green House Gases</i> .....	32
<i>6.4.3. Litter decomposition</i> .....	34
<i>6.4.4. DOC leaching</i> .....	35
<i>6.4.5. Soil organic matter and soil structure</i> .....	36
<i>6.4.6. Other measurements</i> .....	37

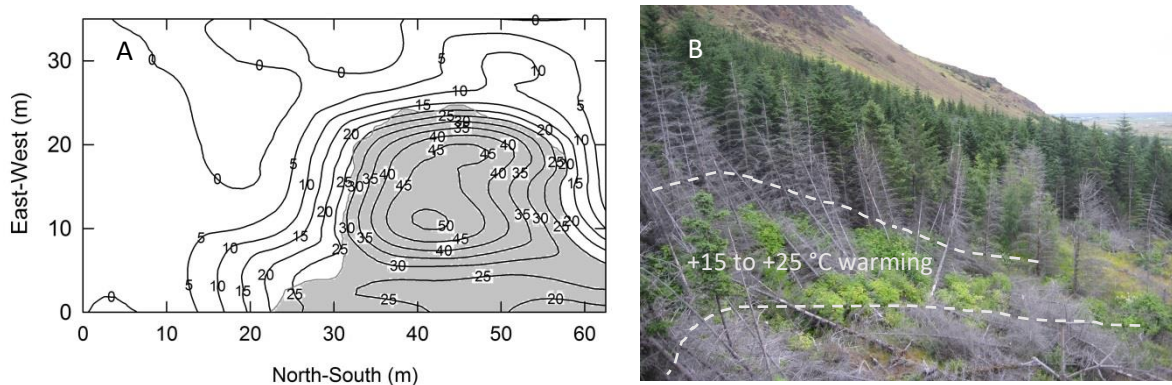
<b>6.5. WP IV: The mortality of the present coniferous trees and their displacement by deciduous ones</b> .....	38
<b>6.5.1. Mapping of temperature changes</b> .....	38
<b>6.5.2. Vegetation succession</b> .....	38
<b>6.5.3. Other measurements</b> .....	41
<b>7. Conclusions and current state of knowledge and future plans</b> .....	42
<b>8. References</b> .....	43
<b>9. Appendices</b> .....	45

This report gives an overview over the **research outputs** (unpublished data, manuscripts and published articles) that the ForHot-Forest project has initiated. Another part of the Final Report gives the economical overview of the project and describes the project's progress in the last half a year (Jan-Jun 2019) and over the whole project time (Jun 2016 – Dec 2019 in terms of milestones and deliverables reached.

## 1. ForHot's experimental setup: short overview

The research site consists of a Sitka spruce forest planted in 1966-1967, on a slope, facing south-west, near the campus of the Agricultural University of Iceland at Reykir in Ölfus (64.008°N, 21.178°W; 100-115 m a.s.l.). The mean annual temperature is 5.3°C and the mean annual precipitation is around 1600 mm. Being planted on ground with normal temperature regime conditions (i.e. non-warmed), a part of the forest got exposed to a gradient of continuous and stable soil warming after the earthquake 29th May 2008, where geothermal systems moved to the bedrock below a previously unwarmed forest area, increasing its soil temperature by radiative heating. A thorough description of the research site can be found in Sigurdsson et al. (2016)

**Figure 1a** shows the warming levels within the forest, where 30 permanent research plots, at five replicated transects with +0 (unwarmed control) and in plots in with ca. +1, +3, +5, +10 and +20 °C mean annual soil temperature had been established before the ForHot-Forest project started. It also took place in three 15 m high scaffolding towers (**see cover photo**), located within the forest stand where the soil temperature is at +0, +3 and +7 °C. This experimental platform (ForHot-Forest) for acquiring knowledge and understanding on the ecosystem response to the soil warming in unique in the world.

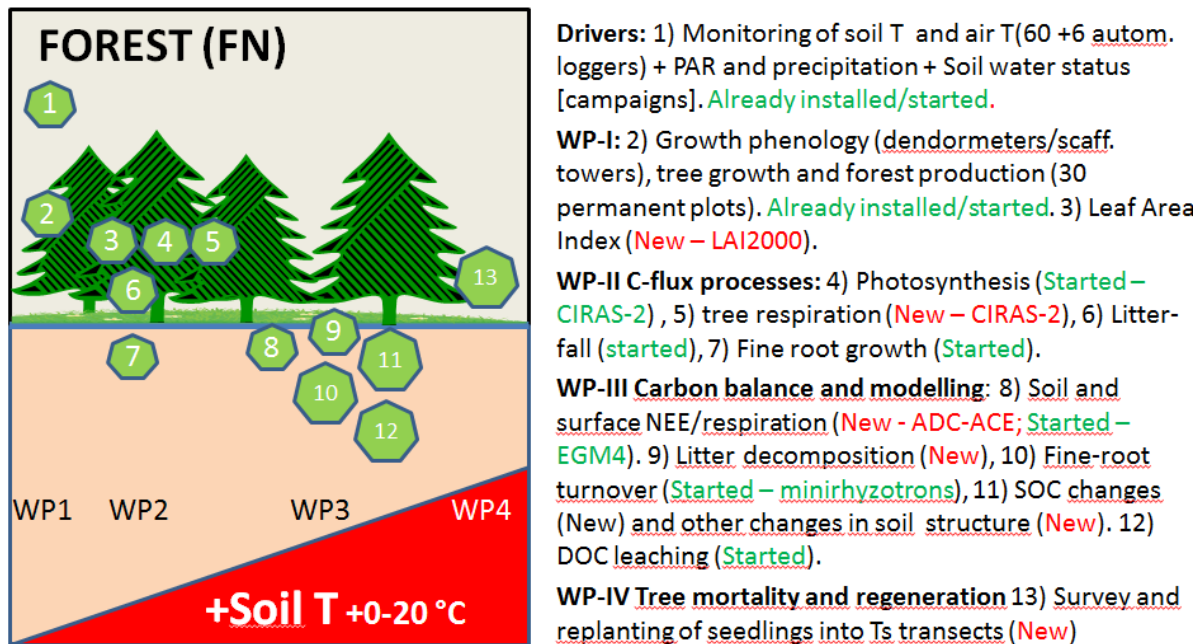


**Figure 1.** a) schematic diagram showing the spatial distribution of geothermal soil warming at the FORHOT forest site. Isolines show differences in soil temperature (°C) at 10 cm depth between unaffected (0 isoline) and warmed areas. The grey area indicates >98% Sitka spruce mortality 4 years after the initiation of the warming (see further in O’Gorman et al., 2014). b) Photo taken from 15 m scaffolding tower in August 2015 into the edge of the spruce dieback area. Note the deciduous tree regeneration appearing where the coniferous trees can not survive, but where soil warming is still less than ca. +30 °C.



## 2. The original research plan

In the original proposal the research project should be in four main Working Packages and 13 key measured processes. **Figure 2** shows a schematic overview how the proposed research was originally and what was the status of the different WPs/key variables at the project's start in spring 2016.



**Figure 2.** Schematic overview about different WPs of the RANNIS-funded activities (PhD student NN1, Proposers and Research Assistant) at the forest site during the project time (2016-2018). Green colour indicates that the activities were already started during 2014-2015 by the co-proposers or various B.Sc. M.Sc. (summer) students or other PhD students (see [www.forhot.is](http://www.forhot.is) / Publications).

The main **objective** of the doctoral project was to study how a stable soil warming of +0 °C to >+20 °C since May 2008 has affected ecosystem structure and function in a middle-aged Sitka spruce (*Picea sitchensis*) stand planted in 1966-1967 in southern Iceland, which has experienced such warming for seven to ten years during the project time (**Figures 1 and 2**).

As partly explained before, then the study took place in already established: a) 30 permanent research plots, at +0 (unwarmed control) and in plots in five replicated transects with ca. +1, +3, +5, +10 and +20 °C mean annual soil temperature and (**Figure 1a and b**) and at three 15 m high scaffolding towers at +0, +3 and +7 °C warming within the stand (**see the cover photo**). Some unpublished data existed also for the site from two and six years following warming.

The four main research questions that were to be addressed in different Work Packages in the original application were:

- I. Is the response in tree growth and areal production of the Sitka spruce linear along the warming gradient?

- Hypothesis: We expect a nonlinear response to warming in both individual tree growth and forest production, with increased growth and NPP with soil warming up to a certain level, but decreases thereafter.
- II. What are the underlying processes for the changes in tree growth and production along the temperature gradient?
  - Hypothesis: Increased production at medium warming will be a result of increased NPP (C-sequestration per unit area), both aboveground and belowground.
- III. How does the forest ecosystem C-balance change across the warming gradient?
  - Hypothesis: The forest will increase its C-sequestration in both biomass and soil at lower warming levels, but higher litter and SOC decomposition rates, leading to both higher soil CO<sub>2</sub> efflux and DOC leaching, will reverse the ecosystem C-balance at higher warming, even before the tree dieback reduces the C-uptake.
- IV. Quantify and study the dieback of the coniferous trees along the five established transects and their replacement by deciduous tree seedlings during the first 10 years since warming started (2008-2017) (**Figure 1b**).

### 3. The time plan of ForHot-Forest

**Table 1.** RANNIS-funded activities at the ForHot forest site during the project time (2016-2018). This includes time plan for the work of the PhD student and the Research Assistant (top), shows timing and different measurements conducted in monitoring and four Work Packages, timing of writing of four main papers of the PhD student and co-authors, timing of Workshops and reporting to RANNIS.

Activities	2016												2017												2018											
	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D
<b>PhD student hired</b>	■	■											■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
ForHot manager in Iceland																																				
Stays at Univ. Antwerp																																				
Research assistant																																				
<b>Monitoring env. drivers</b>																																				
SoilT, Ta, PAR, RH, soil water																																				
<b>WP-I: Tree growth /For. prod.</b>																																				
Dendrometers / Shoot phenol.																																				
Fixed plot measurements																																				
Leaf Area Index*																																				
Root biomass																																				
<b>WP-II: Plant C-fluxes</b>																																				
Photosynthesis																																				
Tree respiration*																																				
Litter fall																																				
Root turnover and production																																				
<b>WP-III: Ecosyst. Carbon balance</b>																																				
Soil respiration																																				
Litter decomposition																																				
DOC leaching																																				
Changes in SOC																																				
Modelling the GPP and C-cycle*																																				
<b>WP-IV: Mortality/regeneration</b>																																				
Survey measurements *																																				
Replanting seedlings *																																				
<b>Synthesis and writing</b>																																				
Paper I																																				
Paper II																																				
Paper III																																				
Paper IIII																																				
<b>General ForHot workshops</b>																																				
Status reports																																				
Final report																																				

\* New WPs initiated by the PhD student

The original time plan for all WPs and the PhD student is shown in **Table 1**. Since there was a delay in when RANNÍS had processed the applications for projects that were to start in 2016, the project did not officially start until June 1, 2016. I.e. there was a six-month delay. This meant that the PhD student was not hired until in autumn 2016 and the whole project was therefore shifted.

#### **4. The modified research plan for the ForHot Forest PhD study**

As always happens in a large research project and doctoral studies, the research questions and focus evolved as the project went forward. When the original research of the doctoral student was presented to the Graduate Study Board of the Agricultural University of Iceland in autumn 2016, it was decided that measurements of CO<sub>2</sub> fluxes and modelling of GPP and Ecosystem Respiration would be outside the PhD project and information on those issues would depend on inputs from other ForHot participants. It was also decided that WP4 would be made a separate student project that would be offered to a BSc/MSc summer student.

It was also decided to put the main focus of the PhD study on measurements of warming-induced changes in both aboveground and belowground NPP (ANPP and BNPP), but especially the latter is little understood.

The main research questions of the ForHot-Forest PhD student (Páll Sigurðsson; **Figure 3**) are on the response in tree growth and areal production; on the underlying processes for the tree growth and production; on how the forest ecosystem carbon-balance changes across the warming gradient; and on the quantification of the dieback of the coniferous trees and their replacement by deciduous woody species.

The papers that are now planned to be a part of the PhD study are:

- I. The effects of elevated soil temperature on above ground growth in Sitka-spruce forest in southern Iceland.
- II. Soil temperature effects on fine-root turnover in a mature Sitka-spruce forest [manuscript ready].
- III. Soil temperature effects on fine-root and aboveground phenology.
- IV. Soil temperature effects on Carbon-stock balance in a mature Sitka-spruce forest in southern Iceland.





*Figure 3 Above: Páll Sigurðsson doing soil sampling. Below: Sampling fine roots in situ and Minirhizotron session.*

## 5. Primary publications and other products from ForHot

Altogether **21** publications have appeared in international journals since the ForHot Forest project started in 2016. Of those, **seven** papers contribute directly to the study on the FORHOT-FOREST project and where **three** papers will or can become part of Páll Sigurðsson's PhD thesis.

Two papers have been published or are in press in *Nature Climate Change* and *Nature Ecosystems and Evolution* – which is a great achievement.

Names of FORHOT-FOREST participants are shown in bold. Publications from the ForHot-Forest project are indicated in blue.

### 2019-2020

#### ForHot-Forest paper:

1. **JOURNAL PAPER:** Christopher Poeplau, **Páll Sigurdsson, Bjarni D Sigurdsson** (2020). Strong warming of a subarctic Andosol depleted soil carbon and aggregation under forest and grassland cover. *Soil* (in press)  
→ This was the second paper directly produced because of the RANNÍS funding of ForHot-Forest and this will also be the second paper in Páll Sigurðsson's PhD thesis. The source (*Soil*) is an open access international journal listed in the ISI database. ForHot-Forest and RANNIS are acknowledged in this paper.
2. **JOURNAL PAPER:** Kaarin Parts, Leho Tedersoo, Andreas Schindlbacher, **Bjarni D. Sigurdsson**, Niki Leblans, **Edda Oddsdóttir**, Werner Borken, **Ivika Ostonen** (2019) Acclimation of fine root systems to soil warming: comparison of an experimental setup and a natural soil temperature gradient. *Ecosystems* 22(3): 457-472.  
<https://doi.org/10.1007/s10021-018-0280-y>  
→ ForHot-Forest and RANNIS are acknowledged in this paper.
3. **JOURNAL PAPER:** Nicholas Rosenstock, Magnus Ellström, **Edda Oddsdóttir, Bjarni D Sigurdsson & Håkan Wallander** (2019). Carbon sequestration and community composition of ectomycorrhizal fungi across a geothermal warming gradient in an Icelandic spruce forest. *Fungal Ecology* 40: 32-42.  
<https://doi.org/10.1016/j.funeco.2018.05.010>  
→ ForHot-Forest and RANNIS are acknowledged in this paper.
4. **JOURNAL PAPER:** Dmitry Kutcherov, Stine Slotsbo, **Bjarni D. Sigurdsson**, Niki I. W. Leblans, Matty P. Berg, Jacintha Ellers, Janine Mariën, and Martin Holmstrup (2020). Temperature responses in a subarctic springtail from two geothermally warmed habitats. *Pedobiologia - Journal of Soil Ecology* (in press).  
→ ForHot-Forest and RANNIS are acknowledged in this paper.

#### Other ForHot papers:

5. **JOURNAL PAPER:** Tom W. N. Walker, Ivan A. Janssens, **Bjarni D. Sigurdsson**, Andreas Richter, Josep Peñuelas, Niki I. W. Leblans, Michael Bahn, Mireia Bartrons, Cindy De Jonge, Lucia Fuchslueger, Albert Gargallo-Garigga, Gunnhildur E. G. Gunnarsdóttir, Sara Marañón-Jiménez, **Edda S. Oddsdóttir, Ivika Ostonen**,

Christopher Poepflau, Judith Prommer, Dajana Radujkovic, Jordi Sardans, **Páll Sigurðsson**, Jenny Soong, Sara Vicca, Hakan Wallander, James T. Weedon & Erik Verbruggen (2020). A systemic decadal-scale overreaction to soil warming in a grassland ecosystem. *Nature Ecology and Evolution* (In press).

➔ It is fantastic to get a paper published in **Nature Ecology and Evolution** from the ForHot project. ForHot-Forest and RANNIS are acknowledged in this paper and the PhD student is a co-author.

6. **JOURNAL PAPER:** Christopher Poepflau, Pierre Barre, Lauric Cecillion, Francois Baudin, **Bjarni D. Sigurdsson** (2019). Changes in the Rock-Eval signature of soil organic carbon upon extreme soil warming and chemical oxidation - A comparison. *Geoderma* 337 (2019): 181-190.
7. **JOURNAL PAPER:** Sara Marañón-Jiménez, Josep Peñuelas, Andreas Richter, **Bjarni D Sigurdsson**, Lucia Fuchslueger, Niki N. I. Leblans, **Ivan A Janssens** (2019). Coupled carbon and nitrogen losses in response to seven years of chronic warming in subarctic soils. *Soil Biology and Biochemistry* 134: 152-161. (<https://doi.org/10.1016/j.soilbio.2019.03.028>).
8. **JOURNAL PAPER:** De Boeck, Hans J.; Bloor, Juliette; Aerts, Rien; Bahn, Michael; Beier, Claus; Emmett, Bridget; Estiarte, Marc; Grünzweig, José; Halbritter, Aud; Holub, Petr; Jentsch, Anke; Klem, Karel; Kreyling, Juergen; Kroel-Dulay, Gyorgy; Larsen, Klaus Steenberg; Milcu, Alexandru; Roy, Jacues; **Sigurdsson, Bjarni**; Smith, Melinda; Sternberg, Marcelo; Vandvik, Vigdis; Wohlgemuth, Thomas; Nijs, Ivan; Knapp, Alan (2019). Understanding ecosystems of the future will require more than realistic climate change experiments – a response to Korell et al. *Global Change Biology* (In press)
9. **JOURNAL PAPER:** Cindy De Jonge, Dajana Radujković, Bjarni D Sigurdsson, James T. Weedon, Ivan Janssens, Francien Peterse (2020). Lipid biomarker temperature proxy responds to abrupt shift in the bacterial community composition in geothermally heated soils. *Organic Geochemistry* (In press) <https://doi.org/10.1016/j.orggeochem.2019.07.006>
10. **JOURNAL PAPER:** Gargallo-Garriga, Albert, Jordi Sardans, Marta Ayala-Roque, Bjarni D. Sigurdsson, Niki I. W. Leblans, Michal Oravec, Karel Klem, Otmar Urban, Ivan Janssens, Josep Penuelas (2020). Effects of warming on the soil metabolome of Icelandic grasslands. *Geoderma* (in press)

## 2018

### ForHot-Forest paper:

11. **JOURNAL PAPER:** Marja Maljanen, Hem Raj Bhattarai, Christina Biasi & **Bjarni D. Sigurdsson** (2018). The effect of elevated soil temperatures on the production of carbon dioxide (CO<sub>2</sub>), methane (CH<sub>4</sub>), nitrous oxide (N<sub>2</sub>O), nitric oxide (NO) and nitrous acid (HONO) from volcanic soils in southern Iceland. *Icelandic Agricultural Sciences* 31, 11-22, doi: 10.16886/IAS.2018.02  
➔ ForHot-Forest and RANNIS are acknowledged in this paper.



### Other ForHot papers:

12. **JOURNAL PAPER:** Tom W. N. Walker, Christina Kaiser, Florian Strasser, Niki I. W. Leblans, Dagmar Woebken, **Ivan A. Janssens, Bjarni D. Sigurdsson** & Andreas Richter (2018). No microbial acclimation despite ecosystem acclimation of soil carbon loss to long term warming. *Nature Climate Change* 8: 885-889.

→ It was fantastic to get a paper published in **Nature Climate Change** from the ForHot project. ForHot-Forest and RANNIS are acknowledged in this paper.

13. **JOURNAL PAPER:** Marañón-Jiménez S., Soong J.L., Leblans N.I.W., **Sigurdsson B.D.**, Peñuelas J., Richter, A., Asensio D., Fransen E., **Janssens I.A.** (2018). Geothermally warmed soils reveal persistent increases in the respiratory costs of soil microbes contributing to substantial C losses. *Biogeochemistry* 138: 245–260. <https://doi.org/10.1007/s10533-018-0443-0>
14. **JOURNAL PAPER:** Martin Holmstrup, Bodil K. Ehlers, Stine Slotsbo, Krassimira Ilieva-Makulec, **Bjarni D. Sigurdsson**, Niki Leblans, Jacintha Ellers and Matty Berg (2018). Resilience in functional diversity of Collembola subjected to long-term warming. *Functional Ecology* 32(5): 1304-1316. doi:10.1111/1365-2435.13058
15. **JOURNAL PAPER:** Dajana Radujković, Erik Verbruggen, **Bjarni D. Sigurdsson**, Niki I. W. Leblans, **Ivan Janssens**, Steven Dauwe, Sara Vicca, James T. Weedon (2018). Prolonged exposure does not increase soil microbial community response to warming along geothermal gradients. *FEMS Microbiology Ecology* 94(2): fix174. <https://doi.org/10.1093/femsec/fix174>

### 2017

#### ForHot-Forest paper:

16. **JOURNAL PAPER:** Marja Maljanen, Heli Yli-Moijala, Christina Biasi, Niki I. W. Leblans, Hans J. De Boeck, **Brynhildur Bjarnadóttir, Bjarni D. Sigurdsson.** (2017). The emissions of nitrous oxide and methane from natural soil temperature gradients in a volcanic area in southwest Iceland. *Soil Biology and Biochemistry* 109: 70-80. <http://www.sciencedirect.com/science/article/pii/S003807171730130X>  
→ ForHot-Forest and RANNIS are acknowledged in this paper.

#### Other ForHot papers:

17. **JOURNAL PAPER:** Marañón-Jiménez S., Soong J.L., Leblans N., **Sigurdsson B.D.**, Peñuelas J., Asensio D., Fransen E., **Janssens I. A.** (2017). Geothermally warmed soils reveal persistent increases in the respiratory costs of soil microbes contributing to substantial C losses. *Biogeochemistry* 138: 245–260. <https://doi.org/10.1007/s10533-018-0443-0>
18. **JOURNAL PAPER:** Gargallo-Garriga, Albert, Marta Ayala-Roque, Jordi Sardans, Mireia Bartrons, Victor Granda, **Bjarni D. Sigurdsson**, Niki I. W. Leblans, Michal Oravec, Otmar Urban, **Ivan A. Janssens** & Josep Peñuelas (2017). Impact of soil warming on the plant metabolome of Icelandic grasslands. *Metabolites* 7(3), 44; doi:10.3390/metabo7030044

19. **JOURNAL PAPER:** Leblans, Niki, **Bjarni D Sigurdsson**, Sara Vicca, Yongshuo Fu, Josep Penuelas, **Ivan Janssens** (2017). Phenological responses of Icelandic subarctic grasslands to short-term and long-term natural soil warming. *Global Change Biology* 23(11):4932-4945. doi: 10.1111/gcb.13749.
20. **JOURNAL PAPER:** Poeplau, Christopher, Kätterer, Thomas, Leblans, Niki I. W., & **Sigurdsson, Bjarni D.** (2017). Sensitivity of soil carbon fractions and their specific stabilisation mechanisms to extreme soil warming in a subarctic grassland. *Global Change Biology* 23: 1316-1327, doi: 10.1111/gcb.13491

## 2016

### ForHot-Forest paper:

21. **JOURNAL PAPER:** **Sigurdsson, B.D.**, N.I.W. Leblans, S. Dauwe, E. Guðmundsdóttir, P. Gundersen, **G.E. Gunnarsdóttir**, M. Holmstrup, K. Ilieva-Makulec, T. Kätterer, B. Marteinsdóttir, M. Maljanen, **E.S. Oddsdóttir**, **I. Ostonen**, J. Peñuelas, C. Poeplau, A. Richter, **P. Sigurðsson**, P.M. Van Bodegom, H. Wallander, J. Weedon and **I. Janssens** (2016). Geothermal ecosystems as natural climate change experiments: the ForHot research site in Iceland as a case study. *Icelandic Agricultural Sciences*, 29: 53-71, doi: 10.16886/IAS.2016.04

→ This was the first paper directly produced because of the RANNÍS funding of ForHot-Forest and this will also be the first paper in Páll Sigurðsson's PhD thesis. The source (IAS) is an open access international journal listed in the ISI database.

ForHot-Forest and RANNIS are acknowledged in this paper



## 6. The research outputs / state of knowledge

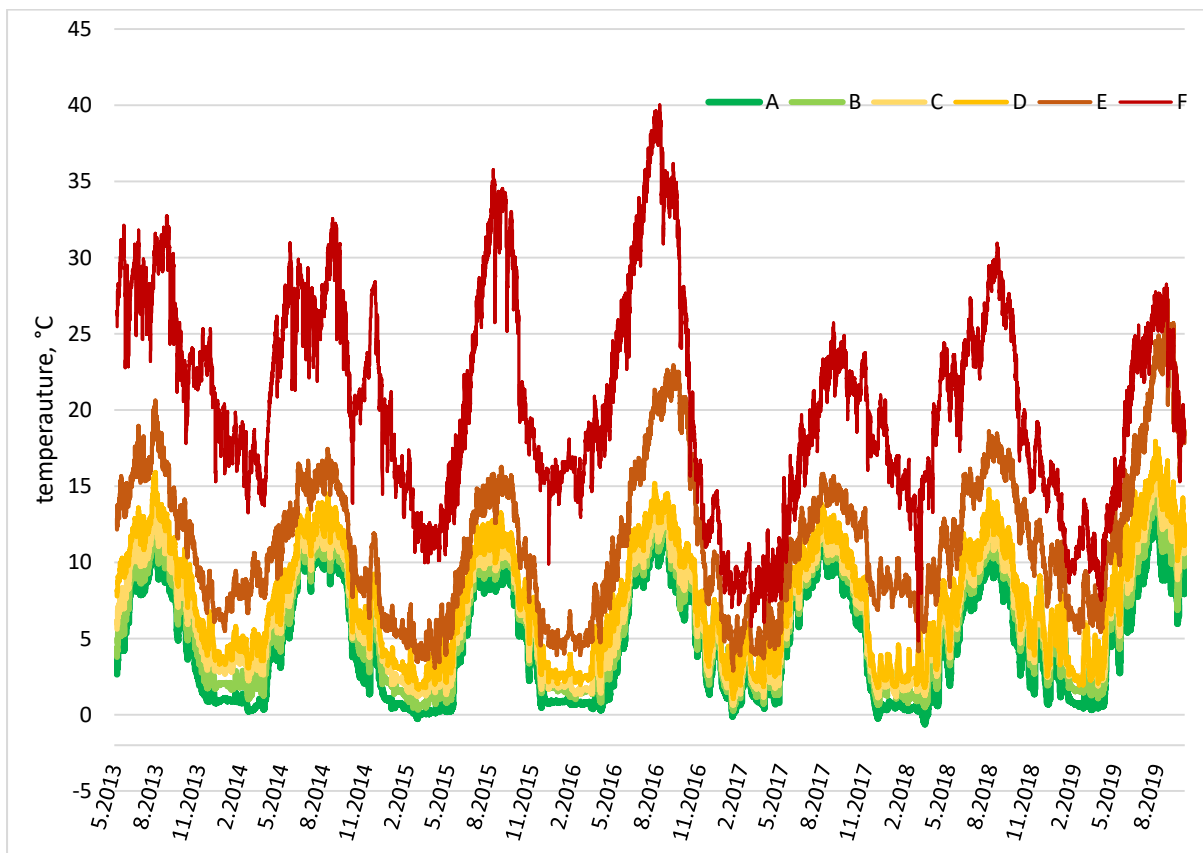
The four main research questions were addressed in corresponding Work Packages (**Table 1**). The works carried out and main results are shown here below.

### 6.1 Monitoring of environmental drivers

Soil temperatures and volumetric soil water content have been monitored throughout the experiment time

#### 6.1.1 Soil temperature

Soil temperatures have been monitored by keeping small temperature loggers in the soil at 10 cm depth in each of the 30 plots in the FN-forest site, logging every hours. Additional loggers are also at 20 cm depth. The mean hourly temperature by gradient (n=5 in each, A = +0°C, B = +1°C, C = +3°C, D = +5°C, E = +10°C and F = +20°C) is shown in **Figure 4**. The mentioned temperatures of the gradients are more of a nominal, and the actual temperature difference can vary slightly between plots in each gradient. The warmest plots, E and F are prone to some more variability, both between plots inside the gradient, as well as trough time. **Table 2** shows the mean annual temperature by gradients and whole calendar years.



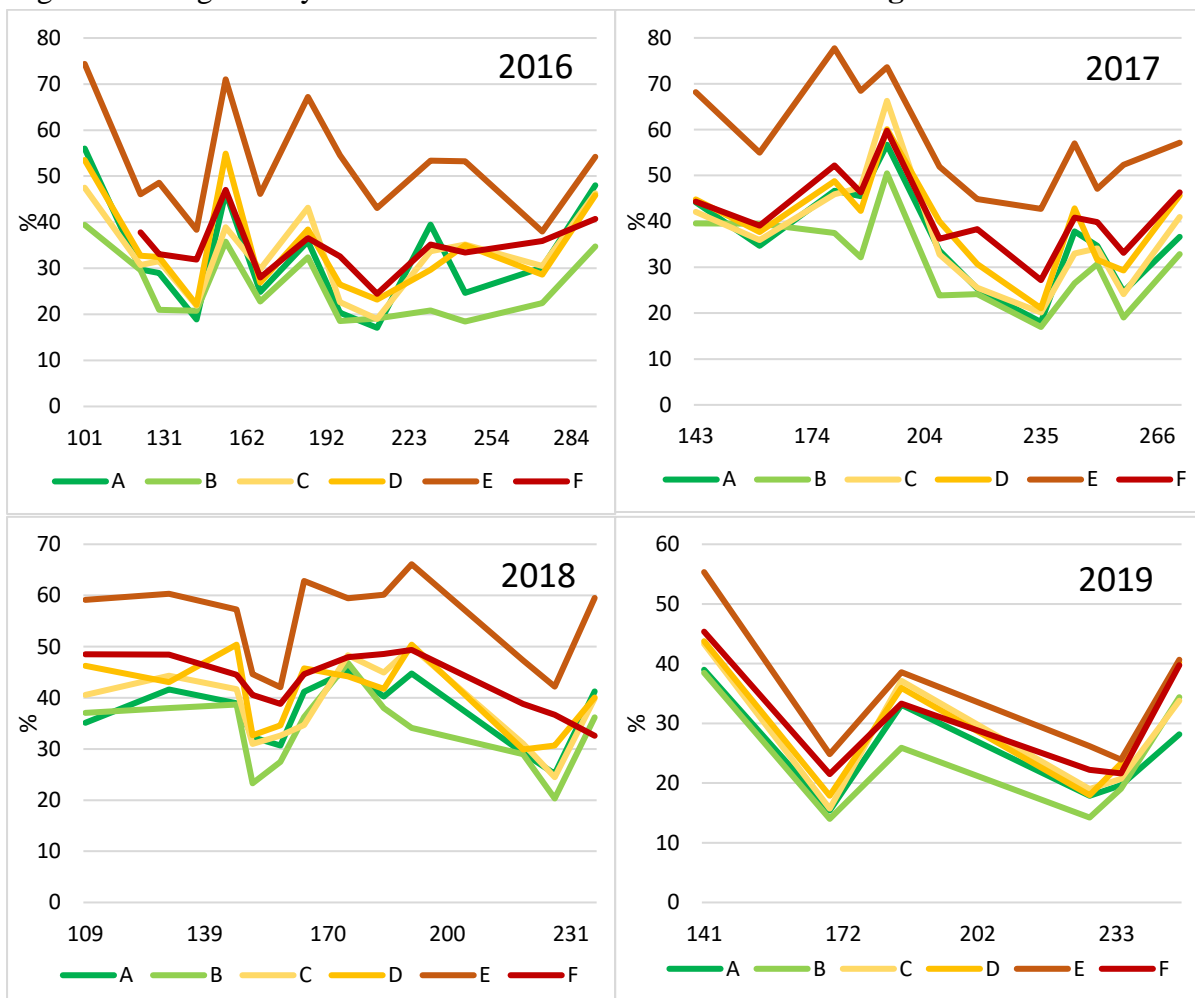
**Figure 4.** Soil temperature by gradients, from May 2013 to September 2019.

**Table 2.** Mean annual soil temperature and standard error, at a 10 cm depth by gradients and years.

year	A	B	C	D	E	F
2014	5.3 ± 0.08	6.2 ± 0.21	7.2 ± 0.21	8.0 ± 0.08	11.1 ± 0.31	22.8 ± 0.99
2015	4.0 ± 0.05	4.8 ± 0.18	5.4 ± 0.11	6.2 ± 0.15	8.7 ± 0.50	19.5 ± 1.13
2016	5.3 ± 0.09	6.1 ± 0.15	6.7 ± 0.14	7.7 ± 0.28	12.2 ± 0.47	22.8 ± 0.66
2017	5.0 ± 0.12	5.8 ± 0.16	6.3 ± 0.12	6.8 ± 0.16	9.6 ± 0.73	15.8 ± 3.15
2018	4.7 ± 0.14	5.8 ± 0.27	6.5 ± 0.24	7.2 ± 0.30	11.9 ± 0.67	20.1 ± 3.56

### 6.1.2 Soil water availability

The volumetric water content has been monitored during the growing season, at a 10 cm depth. In general, the water content is between 20 and 50%, with the soils at the plots in the E-gradient are generally wetter. The water content is visualized in **Figure 5**.

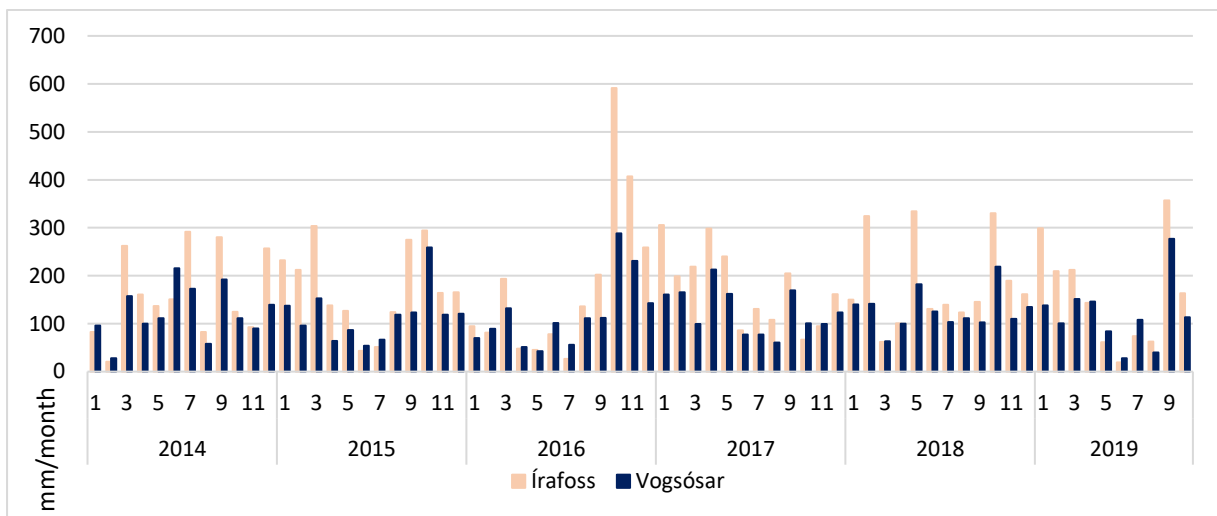


**Figure 5.** Volumetric water content in the soils during the vegetation period (days of year), during the years 2016-2019.

### 6.1.3 Other variables

#### Precipitation

No permanent measurements of precipitation are taking place neither at Reykir nor in the closest neighbourhood. There was a weather station operating at the campus during the years 1971-2000. If compared to a nearby weather station, Írafoss, located 13 km away inland, the difference in precipitation on a yearly basis, during the years the both stations were operating (1981-2000), was generally within 200 mm / year. **Figure 6** shows the monthly precipitation during the years 2014-2019, at two weather stations, Vogsóssar (30 km away, by the seashore), and Írafoss. **Table 3** shows the annual precipitation at the two stations.



**Figure 6.** Monthly precipitation (mm) at the weather stations at Írafoss and Vogsóssar. Data from the Icelandic meteorological office ([www.vedur.is](http://www.vedur.is)).

**Table 3.** Annual precipitation, mm/year, at the two weather stations. Data from the Icelandic meteorological office ([www.vedur.is](http://www.vedur.is)).

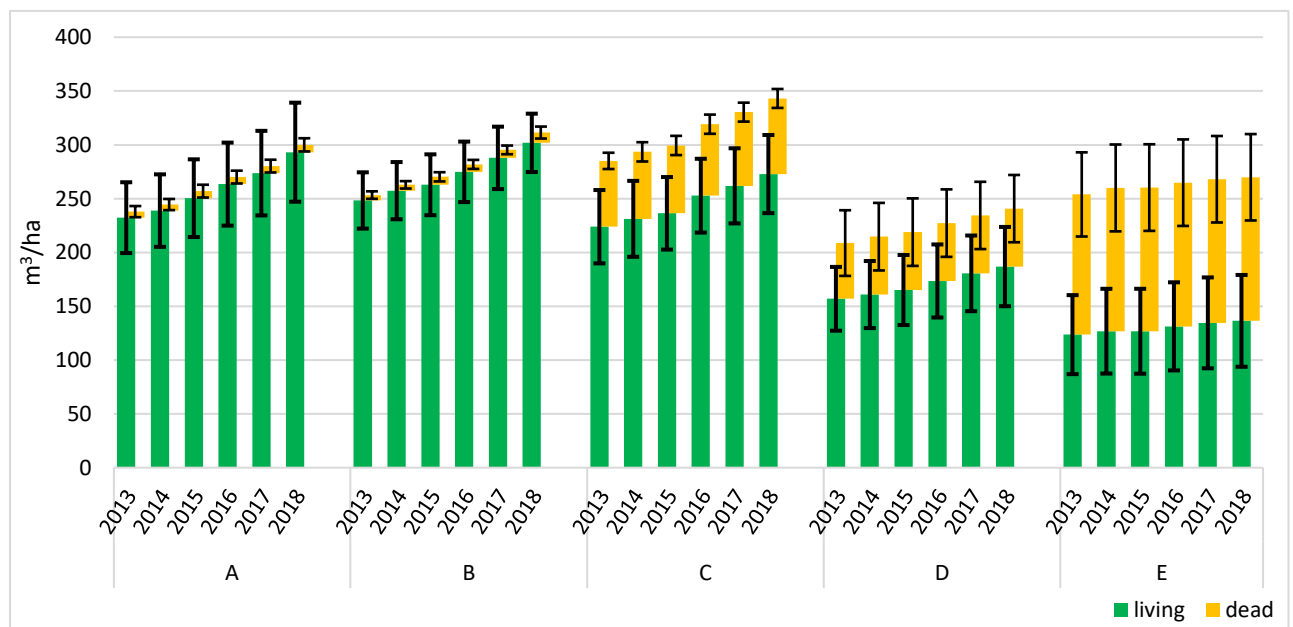
year	2012	2013	2014	2015	2016	2017	2018	2019
Írafoss	2007.2	2079.7	1942.0	2129.9	2160.6	2112.7	2191.0	1601.4
Vogsóssar	1313.6	1498.5	1470.8	1397.6	1426.9	1507.8	1533.0	1185.8

## 6.2 WP I: Tree growth and production response

**Work Package 1** includes structural and quantitative measurements of the changes in the forest stand along the warming gradients. There are thirty-eight permanent 50 m<sup>2</sup> measurement plots in the forest, where diameter (D<sub>1,3</sub>) and living status have been measured between every growing season (and still ongoing), as well as height and height growth of 38 dominant and codominant trees. In every plot there is at least one tree with a dendrometer, to read off diameter growth during the growing season. In three scaffolding towers shoot elongation during the growing season has been measured. Leaf Area Index (LAI) has been measured during one year, in the same time as minirhizotron imaging (see chapter 6.3.2). During the minirhizotron imaging one set of soil cores was taken, to obtain data on fine root biomass (FRB). The cores were washed out and the data is ready. FRB and fine root turnover data from the minirhizotrons are the central components in a ready manuscript on the fine root turnover and biomass [attached].

### 6.2.1 Forest production (C-stock changes)

The changes in standing volume per hectare are shown on **Figure 7**. The addition of dead trees is due to the living trees dying, as they are considered not to change in volume after they are dead, neglecting the actual decaying processes. The trees in the warmer plots (D and E) have believably massively died off during the first years of warming and until the first thorough measurements took place (2008-2013).



**Figure 7.** The volume (m<sup>3</sup>/ha) and standard error, for each soil warming gradient, by years and life status category.

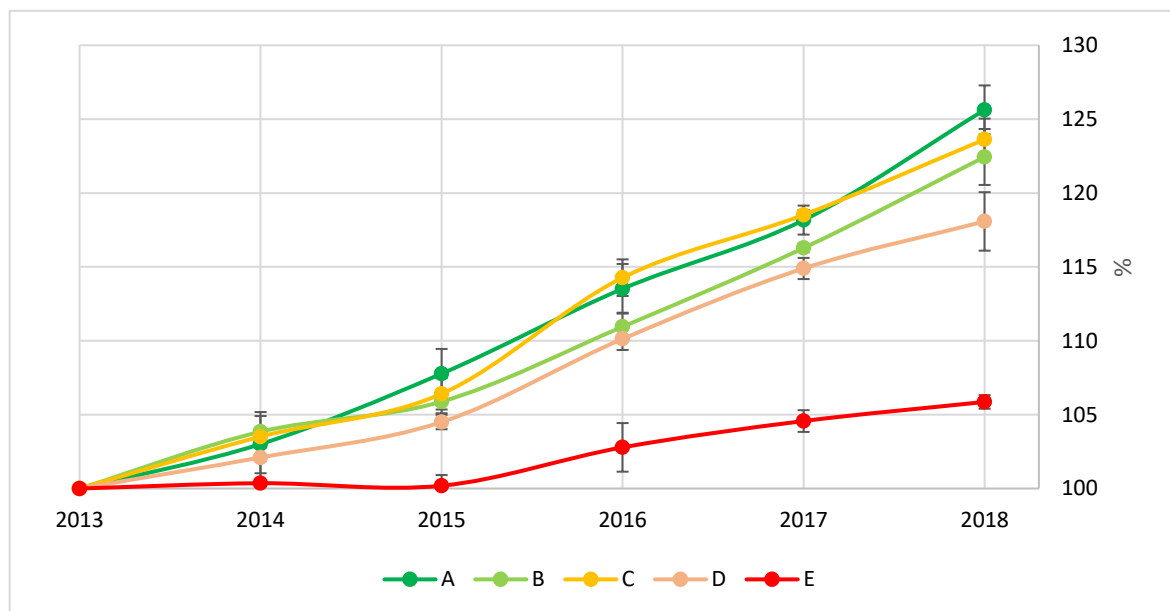
As no forest is totally homogenous by the size and productivity of the trees, the best way to represent the effect of the soil warming on the forest production is to show it as the difference in volume growth in time, proportional to the initial volume. The trees are all in the same age,

and thus should be in the same ontogenical phase of volume increment speed. The measuring of the trees began in 2013, and thus that year is the year of initial volume.

**Table 4** shows the proportional increment of the living spruce trees. Note, that even in the warmest E-gradient, where trees fall from the category of living trees into dead trees, the remaining living trees still manage to keep the overall growth by ~1% per year. The relative changes through the years are shown on **Figure 8**.

**Table 4.** Stem volume ( $m^3/ha$ ) of the spruce trees by living status category and soil warming gradient, the years 2013 and 2018.

Gradient	category of spruce trees	year		$\Delta_{2013-2018}, \%$
		2013	2018	
A	living	232.3 ± 32.91	293.2 ± 46.01	25.9 ± 5.90
	dead	5.6 ± 5.17	6.8 ± 6.14	
B	living	248.3 ± 26.16	301.8 ± 27.12	22.4 ± 2.93
	dead	5.0 ± 3.49	9.5 ± 5.56	
C	living	223.9 ± 34.07	272.8 ± 36.31	23.9 ± 5.49
	dead	61.2 ± 7.58	70.3 ± 8.80	
D	living	156.9 ± 29.64	186.9 ± 36.84	18.0 ± 2.57
	dead	51.8 ± 30.52	53.9 ± 31.27	
E	living	123.6 ± 36.72	136.4 ± 42.64	6.1 ± 4.84
	dead	130.3 ± 39.11	133.4 ± 40.16	

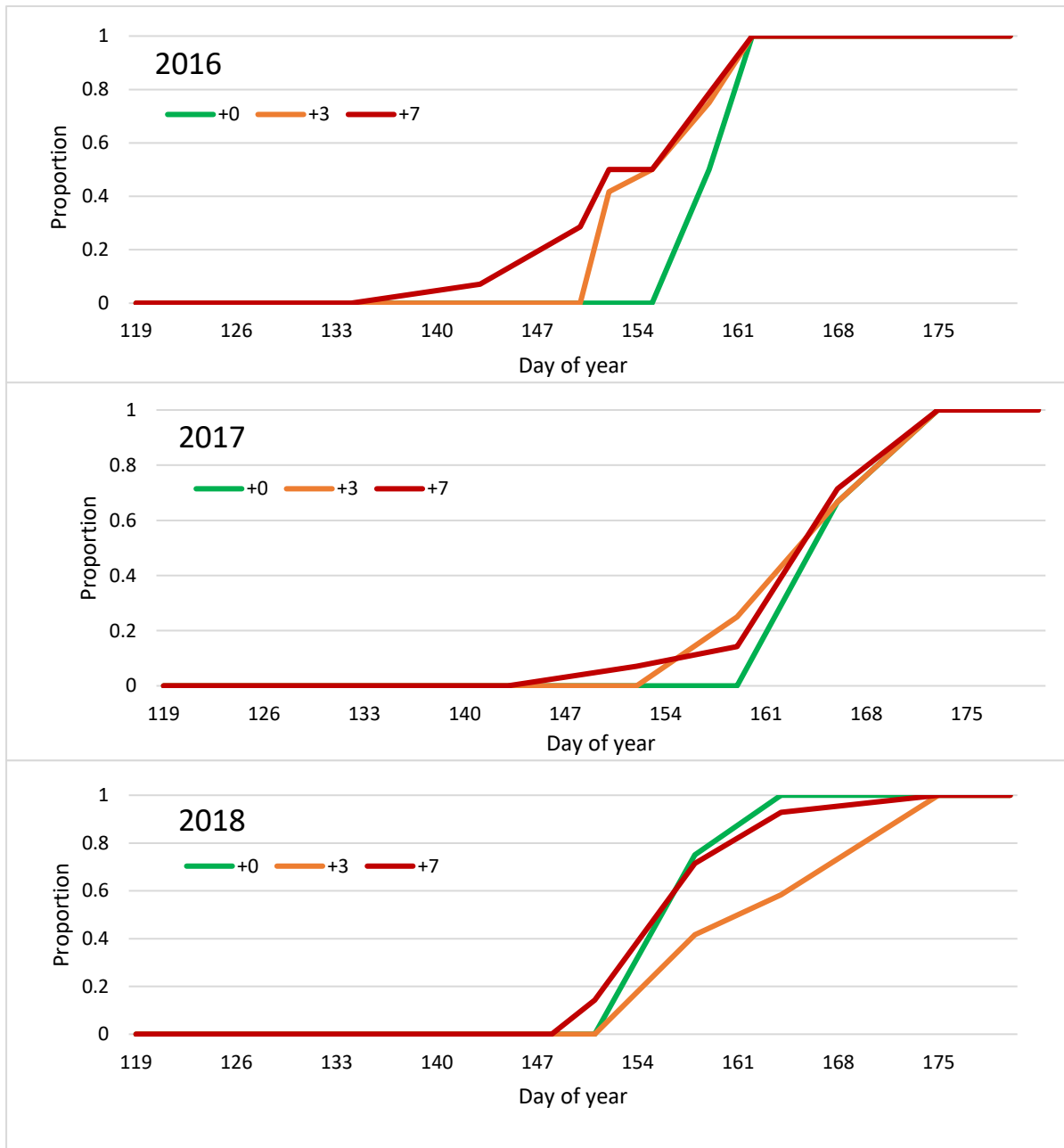


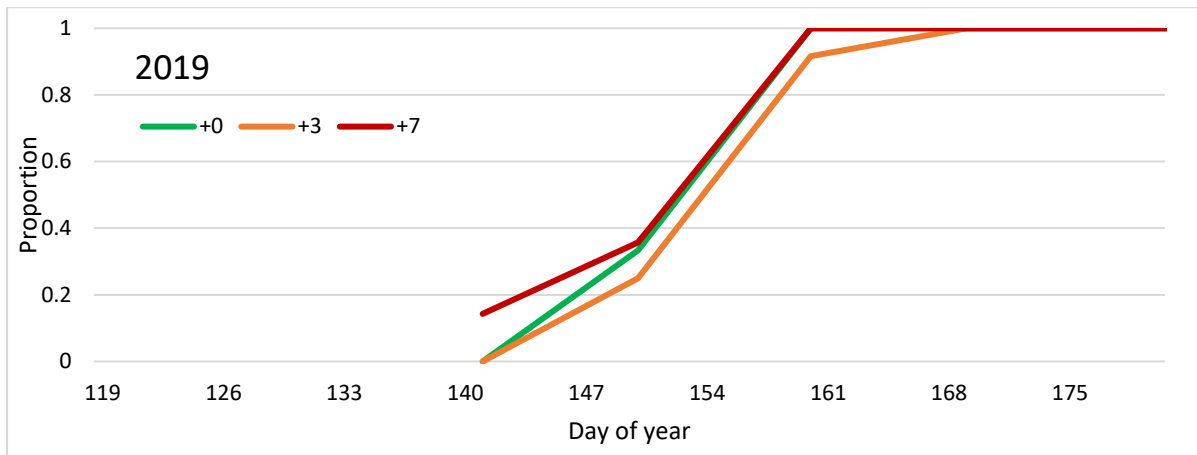
**Figure 8.** Relative changes in stem volume ( $m^3/ha$ ) and standard error, between growing seasons, with the season 2013-2014 as a starting point (100%)



### 6.2.2 Radial growth and height growth phenology

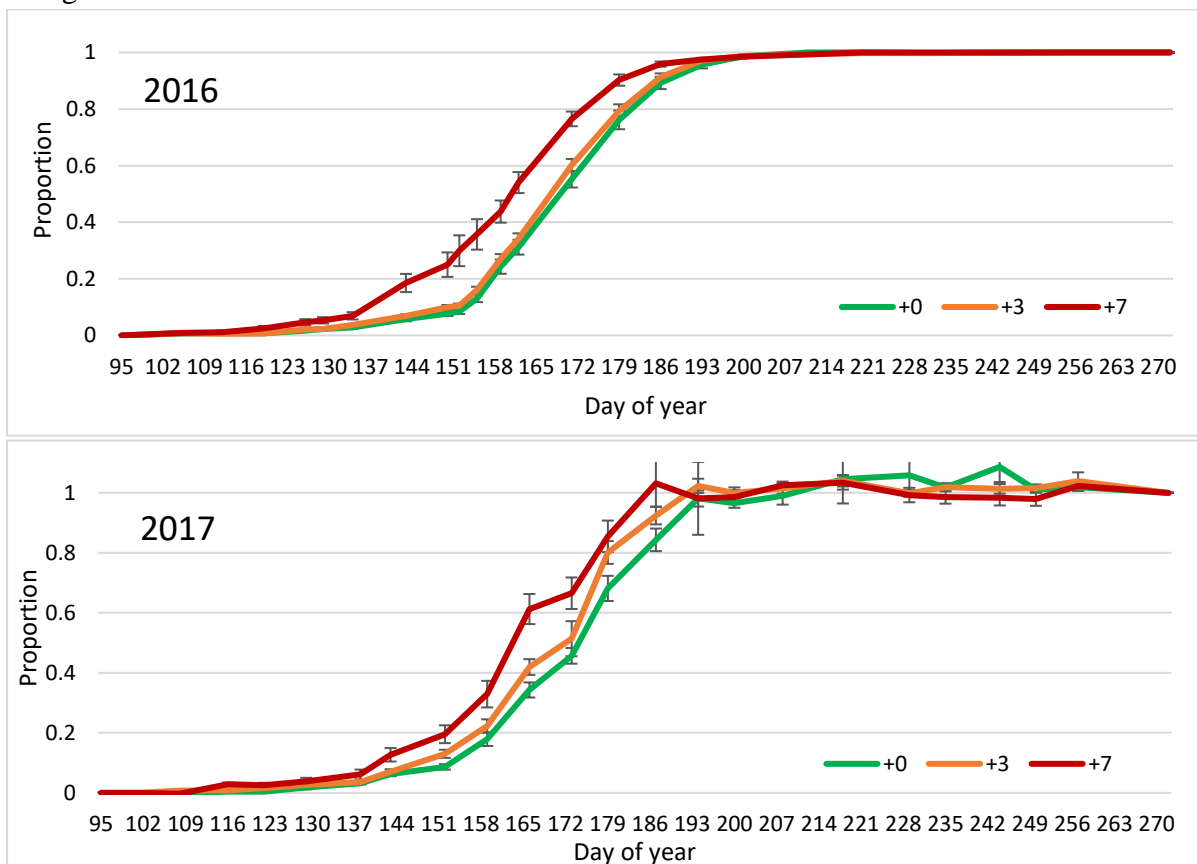
As the shoots start to grow in spring and the endbuds start to swell, they break of the brown scales covering the bud. The timing of the budbreak can thus be used to detect the moment in the shoot growth phenology. The proportion of the measured shoots in the crowns of threes in three towers at different soil warming level is shown in **Figure 9**. The picture varies from year to year, but as expected, the trees at the warmer levels break the buds earlier than the trees at the unwarmed soils.

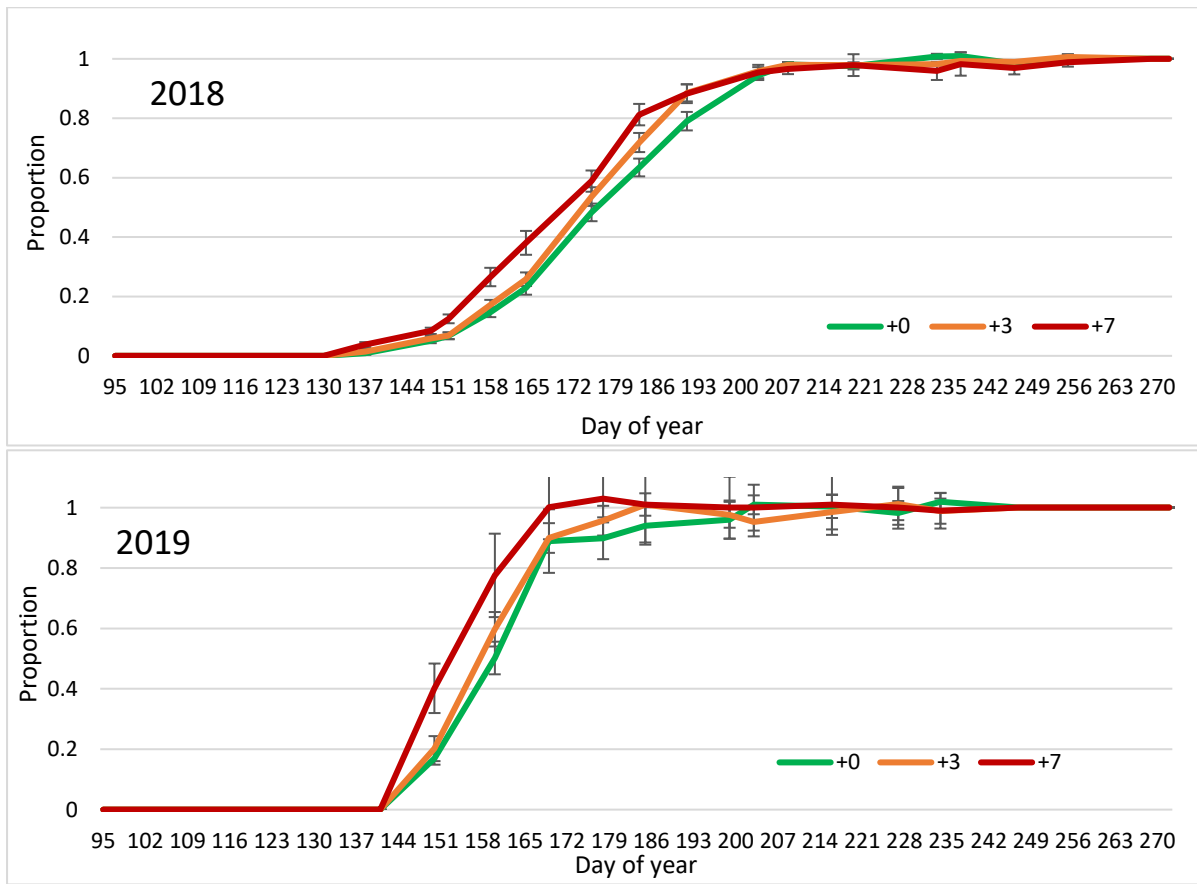




**Figure 9.** Proportion of the shoots' budbreak (day of year), by three soil warming levels.

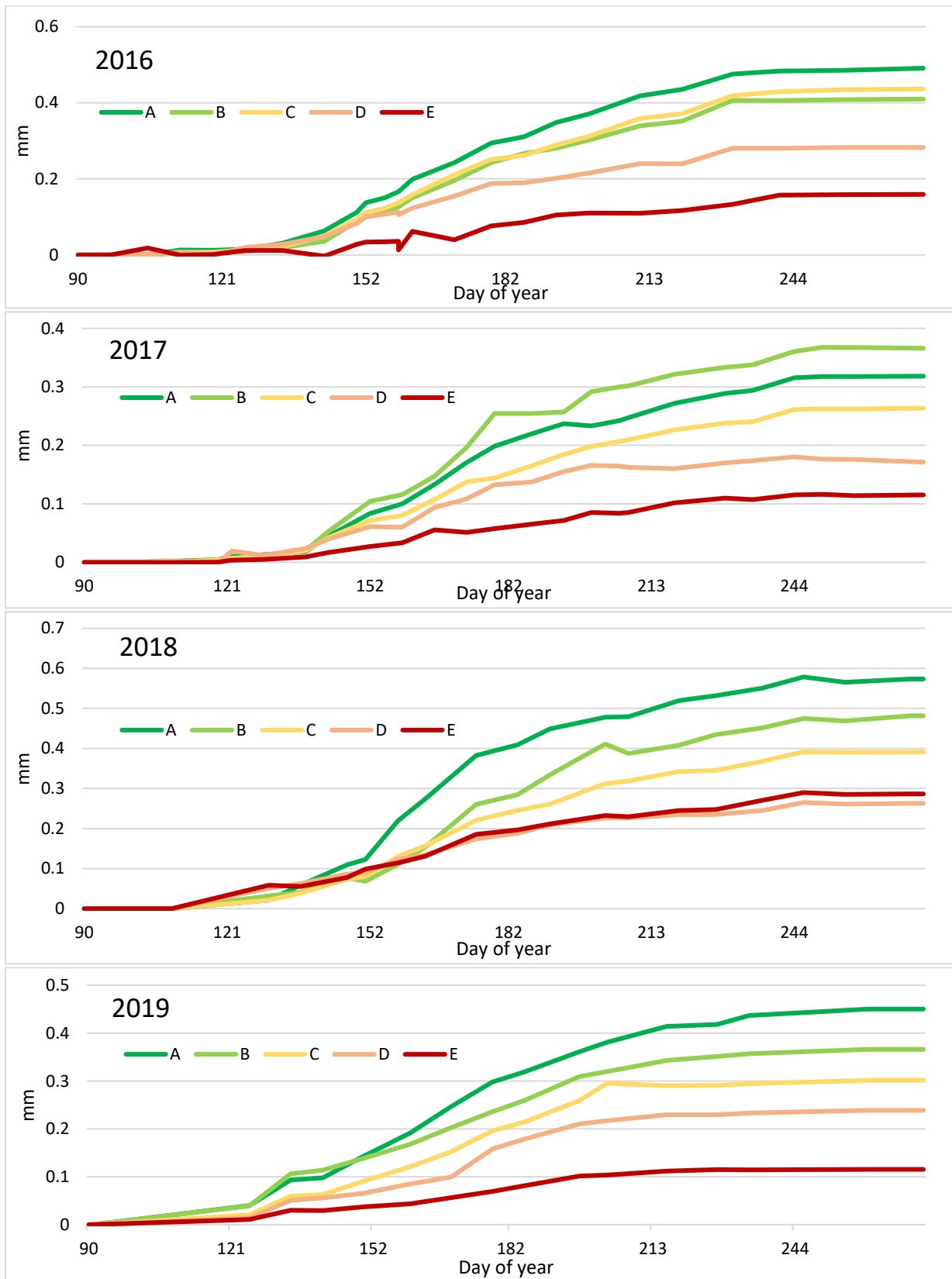
The shoot elongation during the growing season, until full stop, was measured as well (**Figure 10**). The trees in the warmest soils (+7°C) show earlier culmination in the shoot elongation earlier than the trees in the cooler soils.





**Figure 10.** Shoot elongation by day of year, in each tower (+0, +3, +7°C), as the mean proportion of full shoot elongation.

The radial diameter increment during three growing seasons is shown in **Figure 11**. The scale is in absolute mean maximum diameter in the end of the growing season, and therefore the diameter increment the trees reach depends a lot on their size, which does not clearly correlate with the soil warming level. But what can be seen on the figures, is that the start, the culmination and the end of diameter increment is quite similar among the soil warming gradients.



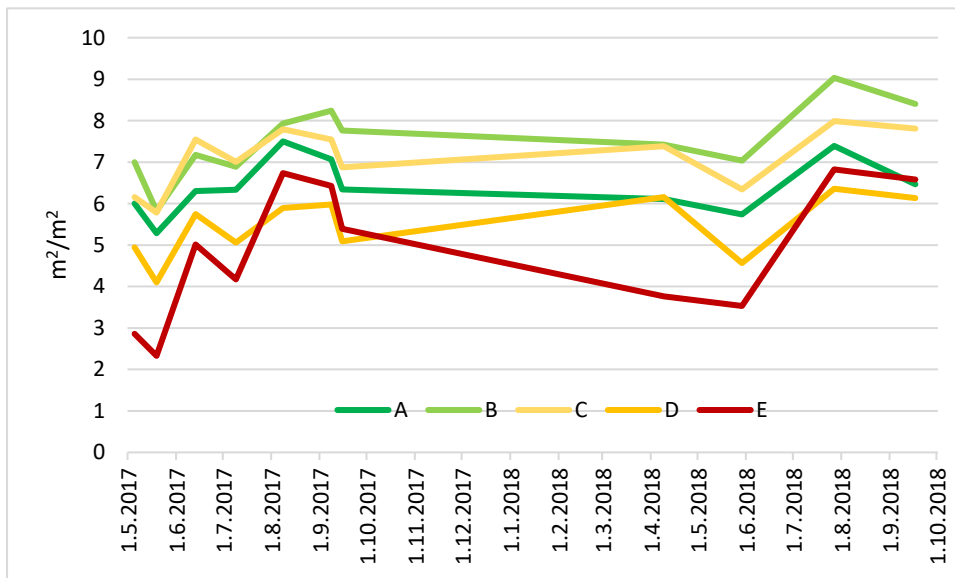
**Figure 11.** Radial diameter increment during three growing seasons (2016, 2017 and 2018), by days of year.

### 6.2.3 Leaf Area Index

The leaf area index (LAI), leaf surface area divided by earth surface area, [ $\text{m}^2/\text{m}^2$ ], is shown in **Table 5** and **Figure 12**. The B- and C-gradients have higher LAI than the A-gradients throughout the year. The steep positive changes in the LAI in the E-gradient in the latter half of the summer are due to deciduous shrub foliage.

**Table 5.** Leaf area index and standard error, throughout the growing season of 2017.

Date gradient	5.5.2017	19.5.2017	13.6.2017	9.7.2017	8.8.2017	8.9.2017	15.9.2017
A	$6.0 \pm 0.18$	$5.3 \pm 0.12$	$6.3 \pm 0.21$	$6.3 \pm 0.19$	$7.5 \pm 0.18$	$7.1 \pm 0.22$	$6.3 \pm 0.20$
B	$7.0 \pm 0.12$	$5.8 \pm 0.09$	$7.2 \pm 0.18$	$6.9 \pm 0.12$	$7.9 \pm 0.15$	$8.2 \pm 0.16$	$7.8 \pm 0.20$
C	$6.2 \pm 0.25$	$5.8 \pm 0.27$	$7.5 \pm 0.28$	$7.0 \pm 0.23$	$7.8 \pm 0.28$	$7.5 \pm 0.32$	$6.9 \pm 0.41$
D	$4.9 \pm 0.18$	$4.1 \pm 0.17$	$5.7 \pm 0.17$	$5.1 \pm 0.23$	$5.9 \pm 0.14$	$6.0 \pm 0.11$	$5.1 \pm 0.10$
E	$2.9 \pm 0.28$	$2.3 \pm 0.20$	$5.0 \pm 0.57$	$4.2 \pm 0.73$	$6.7 \pm 0.70$	$6.4 \pm 0.65$	$5.4 \pm 0.55$



**Figure 12.** Leaf area index throughout two growing seasons.

### 6.2.4 Fine root biomass

Total fine root biomass decreases with increased warming. (**Table 6**). The decrease is more pronounced in the deeper soil layers ( $> 5$  cm).

**Table 6.** Fine root biomass,  $\text{g}/\text{m}^2$ , by soil depth and warming gradients.

warming gradient	soil depth, cm			total
	0-5	5-10	10-27	
ambient (A)	$185 \pm 37.5$	$234 \pm 20.2$	$304 \pm 53.6$	$723 \pm 96.9$
C	$254 \pm 72.8$	$149 \pm 44.0$	$101 \pm 49.3$	$504 \pm 155.5$
D	$233 \pm 72.9$	$114 \pm 28.6$	$95 \pm 38.7$	$442 \pm 129.7$
E	$69 \pm 53.4$	$47 \pm 22.4$	$30 \pm 14.3$	$146 \pm 61.6$



### 6.3 WP II: Plant carbon fluxes

The research question is: (II) What are the underlying processes for the changes in tree growth and production along the temperature gradient? **Work Package 2** consists of measuring plant carbon fluxes in and out of the ecosystem, and includes gas exchange measurements and both aboveground and belowground litterfall.

Aboveground litterfall has been sampled from 60 litter traps since 2014 and the data is under process (**Table 7**). Belowground litterfall is measured by Minirhizotron tubes (**Figure 3**). They were installed in the autumn 2013, the first images were captured in spring 2015 and regular imaging started in January 2017. The images have been analysed and interpreted. For comparing with the minirhizotron data, root ingrowth bags were inserted in the spring 2014 and extracted in 2017.

#### 6.3.1 Aboveground litter fall

As shown in **Table 7**, the needle litterfall is quite variable between gradients, being highest in the D-gradient (+5°C), but lowest in the warmest E-gradient. Litterfall of leaves is evidently higher in the E-gradient, as deciduous shrubs are more pronounced there, replacing the dying spruces (see chapter 6.5.2.).

**Table 7.** Aboveground litterfall,  $g/m^2 \pm SE$ , over the year June 2016 - June 2017, according to soil warming gradients. Different letters indicate significant difference.

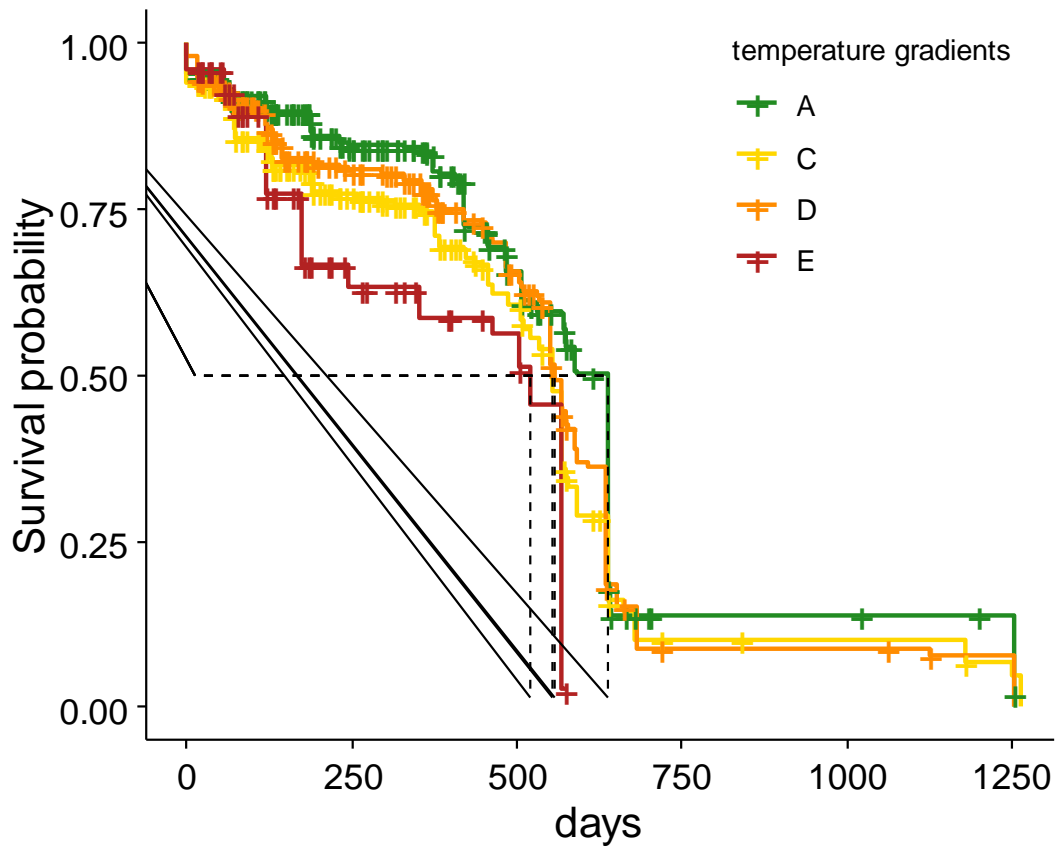
gradient	LF <sub>needles</sub>	LF <sub>leaves</sub>	LF <sub>branches</sub>	LF <sub>total</sub>
A	103.9 <sup>c</sup> ± 11.34	2.9 <sup>c</sup> ± 1.02	49.2 <sup>b</sup> ± 16.88	156.0 <sup>b</sup> ± 19.50
B	128.2 <sup>c</sup> ± 16.26	0.6 <sup>a</sup> ± 0.27	28.7 <sup>a</sup> ± 5.68	157.5 <sup>b</sup> ± 21.53
C	85.4 <sup>b</sup> ± 4.05	2.2 <sup>c</sup> ± 1.18	20.1 <sup>a</sup> ± 3.38	103.0 <sup>a</sup> ± 5.29
D	176.2 <sup>d</sup> ± 20.97	0.7 <sup>b</sup> ± 0.33	24.5 <sup>a</sup> ± 5.98	201.4 <sup>c</sup> ± 23.06
E	52.7 <sup>a</sup> ± 25.29	12.6 <sup>d</sup> ± 5.81	29.5 <sup>a</sup> ± 6.03	90.9 <sup>a</sup> ± 23.55

#### 6.3.2 Fine root turnover and production

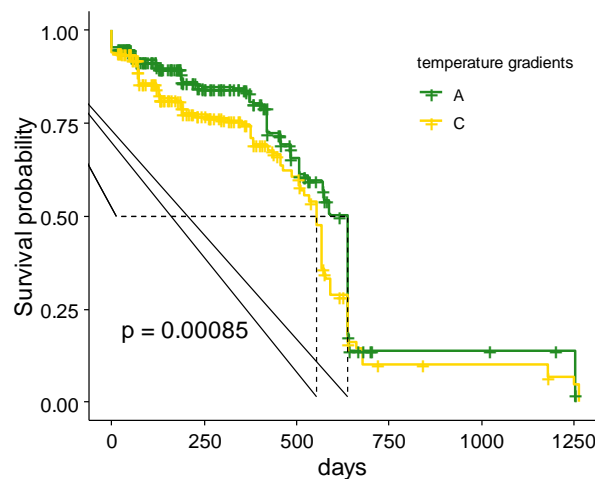
The root turnover rate has been estimated from the minirhizotrons by median survival of the fine roots, by Kaplan-Meier survival function. Turnover is then calculated as the inverse of the survival. The median survival rate is highest in the unwarmed plots - 639 days. The longevity decreases with warming from the control, but does not decrease significantly with more severe warming (**Table 8** and **Figures 13-16**).

**Table 8.** Fine root longevity (days) in four warming gradients. The median longevity (95% confidence limits) estimated by Kaplan-Meier survival function.

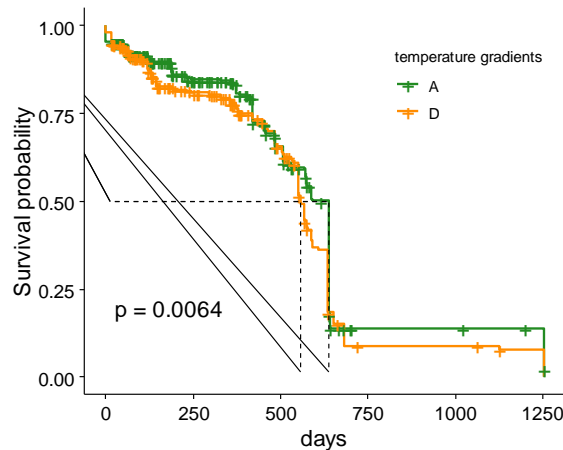
	A	C	D	E
Median (Kaplan-Meier)	639 (573-639) <sup>a</sup>	553 (519-566) <sup>b</sup>	556 (551-576) <sup>b</sup>	519 (351-566) <sup>b</sup>
Number of roots	477	331	334	107



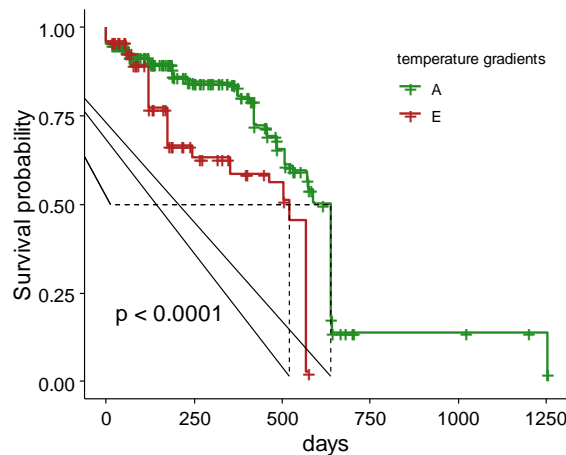
**Figure 13.** Kaplan-Meier survival curves for Sitka spruce fine roots of each warming gradient. Ambient soil temperature (A) – green; +1.4 C° warming (C) – yellow; +1.9 C° warming (D) – orange and +4.7°C warming (E) – red.



**Figure 14.** Kaplan-Meier survival curves for Sitka spruce fine roots of two warming gradients, ambient soil temperature (A) – green and +1.4 C° warming (C) – yellow.



**Figures 15.** Kaplan-Meier survival curves for Sitka spruce fine roots of each warming gradient. Ambient soil temperature (A) – green and +1.9 C° warming (D)– orange.



**Figures 16.** Kaplan-Meier survival curves for Sitka spruce fine roots of each warming gradient. Ambient soil temperature (A) – green and +4.7°C warming (E) – red.

By dividing one year by the mean longevity, the fine root turnover rate can be found. The annual fine root turnover is  $0.57 \text{ year}^{-1}$  for the unwarmed control,  $0.66 \text{ year}^{-1}$  for the C plots,  $0.66 \text{ year}^{-1}$  for the D plots and  $0.70 \text{ year}^{-1}$  for the warmest E plots. Multiplied by the fine root biomass (FRB) (**Table 6**), the turnover rate can be represented in absolute numbers of fine root production (FRP). Annual fine root production is  $412 \text{ g/m}^2/\text{year}$  in the unwarmed control (A),  $333 \text{ g/m}^2/\text{year}$  in the C-plots,  $292 \text{ g/m}^2/\text{year}$  in the D-plots and  $102 \text{ g/m}^2/\text{year}$  in the E-plots.

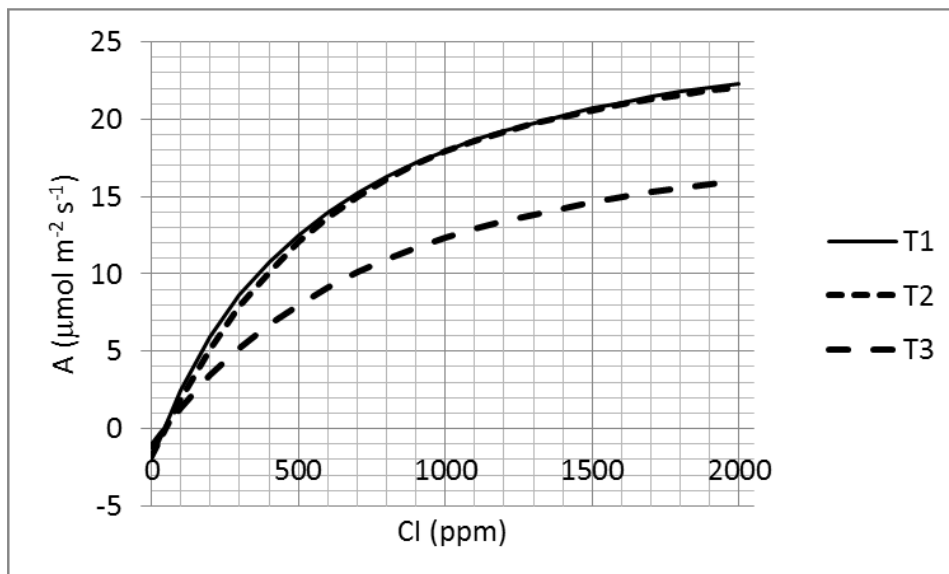
Another method to estimate fine root turnover is the ingrowth method (IG). According to fine root ingrowth nets (2014-2016, unpublished data from Edda S. Oddsdóttir) the turnover rates are comparable: for the ambient plots (A):  $0.70 \text{ year}^{-1}$ ; for the C-plots:  $0.68 \text{ year}^{-1}$ ; for the D-plots:  $0.42 \text{ year}^{-1}$ , only the warmest plots (E) showed almost twice higher turnover rate than estimated by the minirhizotrons:  $1.33 \text{ year}^{-1}$ . Using turnover rate that is calculated as relative proportions only,  $(\text{FRP}_{1\text{yr}} / \text{average}(\text{FRP}_{1\text{yr}}; \text{FRP}_{2\text{yr}}))$ , the FRP was calculated by multiplying

turnover rate<sub>(IG)</sub> with fine root biomass. The FRP calculated from ingrowth nets was in ambient plots (A): 503 g m<sup>-2</sup> yr<sup>-1</sup>; in the C-plots 343 g m<sup>-2</sup> yr<sup>-1</sup>; in the D-plots 184 g m<sup>-2</sup> yr<sup>-1</sup> and in the warmest, the E-plots 195 g m<sup>-2</sup> yr<sup>-1</sup>.

### 6.3.3 Photosynthesis

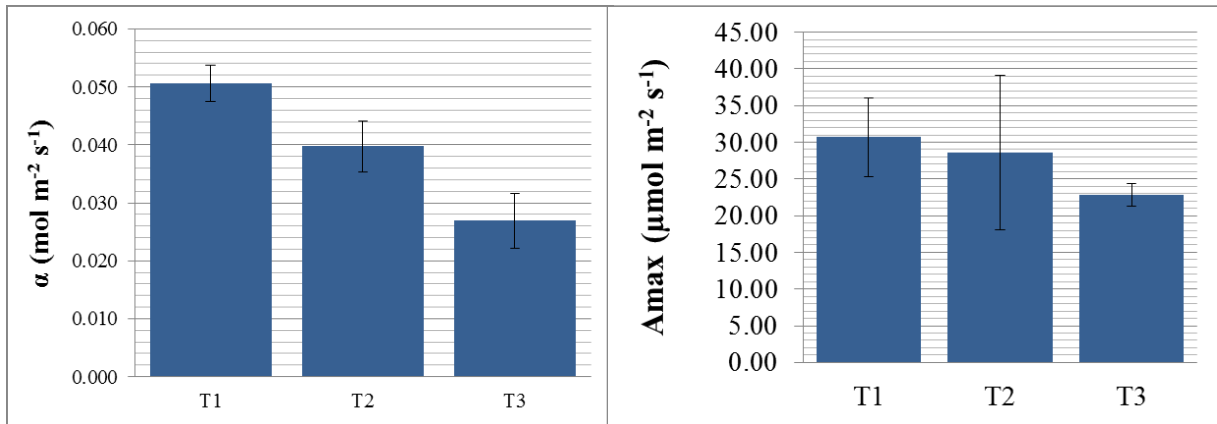
A/Ci-, light- and temperature-response curves of net-photosynthesis, as well as measurements of seasonal changes in light-saturated net photosynthesis ( $A_{\text{sat}}$ ), stomatal conductance ( $g_s$ ) and wood respiration ( $R_t$ ) rate all give different insights into the carbon uptake (GPP) and the net ecosystem exchange (NEE) of the ecosystem. To better understand the reasons for changing  $A_{\text{sat}}$  fluxes, needle nutrient contents are determined by chemical analysis.

The A/Ci-, light- and temperature-response curves of net-photosynthesis, light-saturated net photosynthesis, stomatal conductance and dark (shoot) respiration rates have been measured, and the results can be found in André & Bondesson (2014). The needle nutrient content has been measured, unpublished. The relation between photosynthesis rate ( $A$ ) and foliar intercellular carbon dioxide concentration ( $C_i$ ) is shown in A/Ci-response curves. A mean of the A/Ci-response curves was made for the trees at soil temperatures +0°C, +3°C and +7°C over ambient (**Figure 17**).



**Figure 17.** Mean A/Ci-response curves for one year old shoots of spruce, growing at an ambient soil temperature (T1), +3°C (T2) and +7°C (T3).

Clearly the trees growing in the warmer soils (T3) had a lower photosynthetic activity, but no major differences were found on the between the trees that grow at ambient soil temperature and around +3°C. When this data is combined with the LAI data (**Table 5, Figure 12**), total C uptake (GPP) can be estimated.



**Figure 18.** Left – carboxylation efficiency ( $\alpha$ ). Right – the estimated maximum photosynthesis rate, in the trees growing in three different soil warming levels - ambient soil temperature (T1), +3°C (T2) and +7°C (T3).

The photosynthetic enzyme efficiency shown on **Figure 18** (left) tells that even if there is not much difference in photosynthetic capacity on **Figure 17**, there are significant shifts in enzymatic adaptations. The carboxylation capacity (maximum activity of the Rubisco enzyme) significantly differs only between the lowest and highest temperature levels, and the maximum photosynthesis rate ( $A_{max}$ ; which indicates the light harvesting systems in the chlorophyll) does not significantly differ between the treatments.

### 6.3.4 Respiration

#### Wood respiration

This variable is the only one that was listed in the original research plan that has not been measured so far.

#### Foliar respiration

Foliar respiration under light-saturated conditions ( $R_{day}$ ) was derived from measured A/C<sub>i</sub>-response curves by the equation

$$A_{sat} = \frac{\alpha C_i + A_{max} - \sqrt{(\alpha C_i + A_{max})^2 - 4\alpha C_i A_{max} \theta}}{2\theta} - R_{day}$$

where  $A_{sat}$  – light saturated photosynthetic rate,  $\mu$ mol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>;  $\alpha$  – carboxylation efficiency,  $\mu$ mol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>;  $A_{max}$  – maximum photosynthetic rate,  $\mu$ mol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>;  $\theta$  - convexity, that shows how steep the curve is;  $R_{day}$  – foliar respiration during daytime,  $\mu$ mol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>. The mean respiration rate ( $R_{day}$ ) was  $1.63 \pm 0.18 \mu$ mol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>. No significant difference was detected between the trees in the three different soil temperature levels.

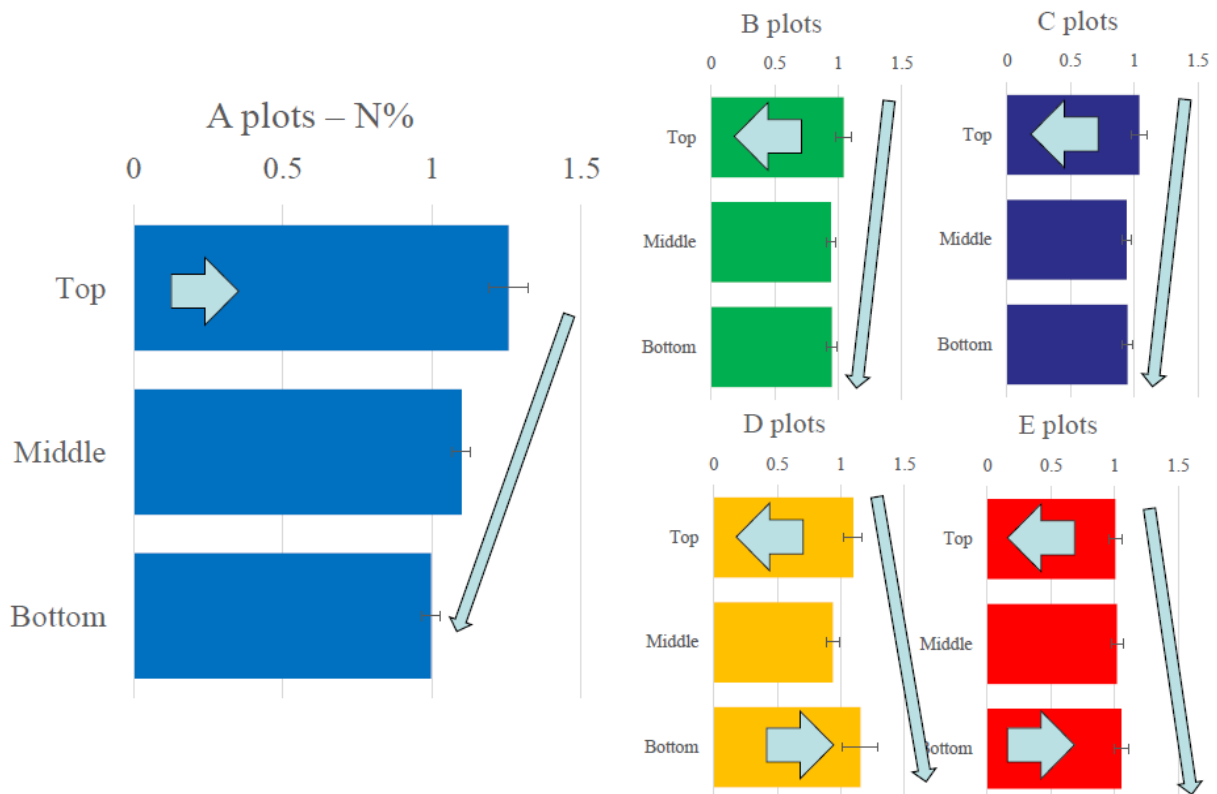
### 6.3.5 Other measurements

#### Specific Needle Area

Specific Needle (leaf) Area [ $\text{cm}^2/\text{g}$ ] of the spruces was measured in 2014 (André & Bondesson, 2014), and again in 2017. No significant difference was detected between soil warming levels, and was average  $40.0 \pm 1.2 \text{ cm}^2/\text{g}$ . When coupled with needle N concentration, the specific needle area of the needles in the lowest third of the tree crowns changes with N concentration, which points to a N-limited stronger shade response (Bjarni D. Sigurðsson, unpublished).

#### Needle nutrient content

Branches were sampled in March 2017, in lowest, middle, and top thirds of the tree crowns. The needle N-content optimum in *Picea sitchensis* is considered to be not less than 1.5% of dry matter; the N-content in the needles of the trees growing in the A-gradient lowers from the top to the bottom of the crown, so does it in the B and C gradients, though they have lower N-content overall (**Figure 19**).



**Figure 19.** Needle N-content in the three parts of the crown. Arrows indicate differences in N-contents.

The concentration of other chemical elements was also determined, in the needles in the crown overall (**Table 9**).

**Table 9.** Needle content of chemical elements as X:N ratios, mean by gradient and standard error.

element	gradient					P-value
	A	B	C	D	E	
P	0.24 ± 0.02	0.2 ± 0.01	0.21 ± 0.02	0.18 ± 0.01	0.2 ± 0.01	0.11
K	0.85 ± 0.04	0.86 ± 0.03	0.76 ± 0.04	0.81 ± 0.04	0.8 ± 0.02	0.3
S	0.13 ± 0.01	0.13 ± 0.01	0.13 ± 0	0.13 ± 0	0.13 ± 0.01	0.97
Mg	0.14 ± 0.01	0.12 ± 0.01	0.13 ± 0.01	0.12 ± 0	0.12 ± 0.01	0.23
Ca	0.62 ± 0.05	0.58 ± 0.05	0.58 ± 0.09	0.53 ± 0.05	0.41 ± 0.06	0.26
Mn	0.022 ± 0.003	0.03 ± 0.003	0.036 ± 0.004	0.037 ± 0.003	0.033 ± 0.004	0.05
Zn	0.004 ± 0	0.003 ± 0	0.003 ± 0	0.003 ± 0	0.003 ± 0	0.47
Cu	0.0003 ± 0.00	0.0003 ± 0.00	0.0002 ± 0.00	0.0003 ± 0.00	0.0003 ± 0.00	0.89



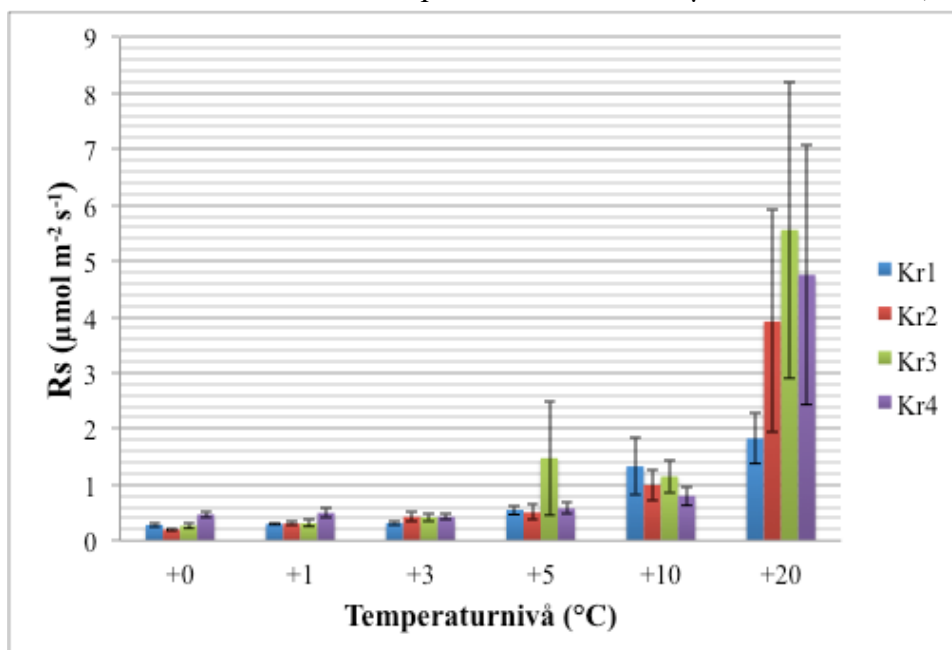
## 6.4 WP III - Ecosystem C-balance

The research question is: (III) How does the forest ecosystem C-balance change across the warming gradient? **Work Package III** handles ecosystem C-balance and modelling. Soil respiration is measured, and changes in litter decomposition rates are estimated by litter bags with *in situ* litter. The flux of dissolved organic carbon (DOC) was estimated by chemically analysing water collected from lysimeters. Soil organic carbon (SOC) contents and other basic soil parameters are also measured.

Soil respiration has been measured (André & Bondesson, 2014) along the soil temperature gradient, and the litter bags have been incubated (unpublished). The DOC from the lysimeter-sampled water has been estimated (unpublished). Soil samples were taken from each permanent plot and divided into forest floor, and the soil layers of 0-5, 5-10, 10-20 and 20-30 cm depth, chemically analysed to determine changes in SOC and other basic soil parameters along the soil temperature gradient, such as stoniness and C/N ratio. As the soil samples were not suitable for determining soil bulk density, another sampling for that has been specially carried out. The data analysis is in process.

### 6.4.1. Soil respiration

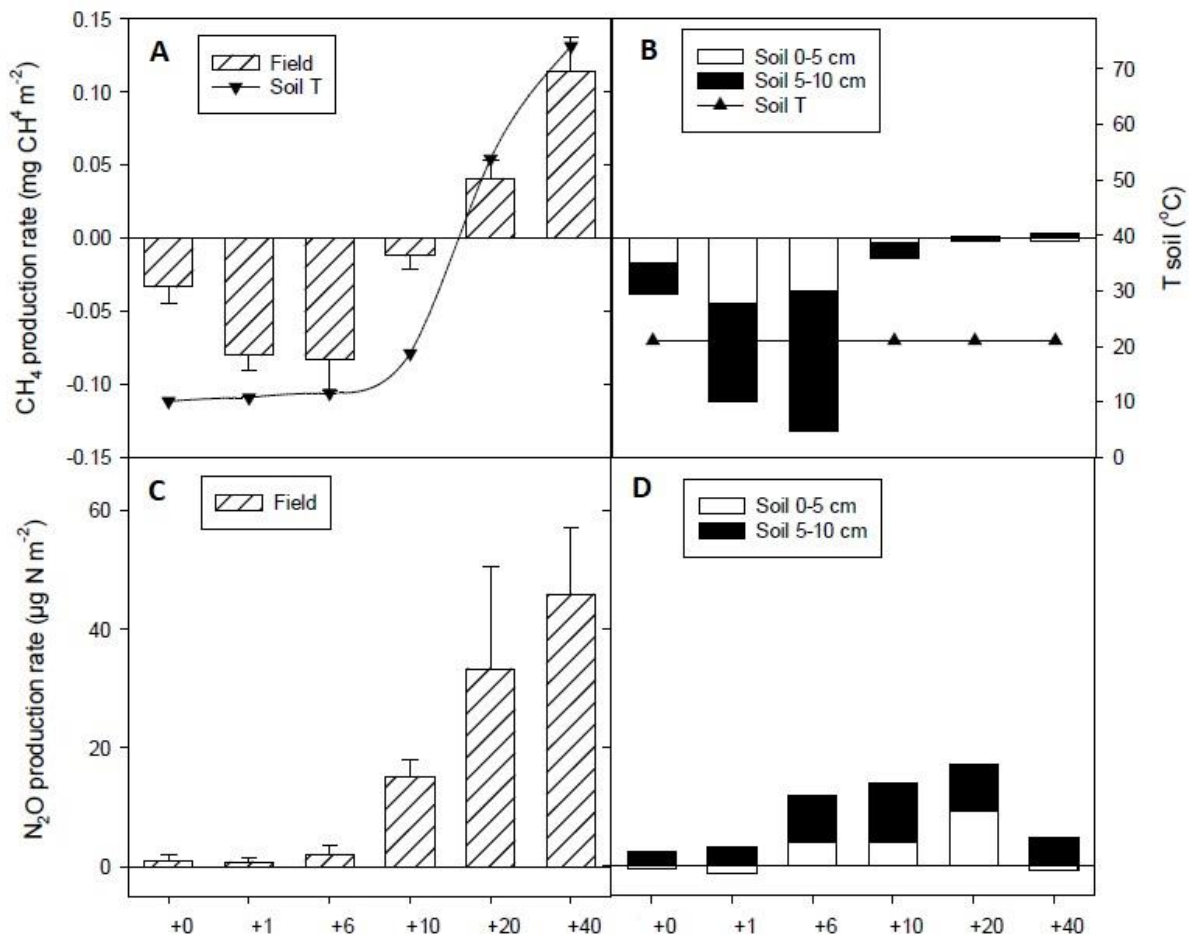
Soil respiration ( $R_s$ ) consists of respiration from decomposition processes in the soil, and root respiration. Soil respiration was measured during 4 measuring campaigns from April 22 to June 3 2014 (André & Bondesson, 2014). No significant differences were observed between the campaigns. The soil respiration rate was lowest in the ambient warmed soil,  $0.30 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , with no significant difference between temperature levels, except between the  $+10^\circ\text{C}$  and  $+20^\circ\text{C}$ , where the respiration rate was  $4.0 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  (**Figure 20**).



**Figure 20.** Soil respiration rates ( $R_s$ ) at different soil temperature levels. Different coloured bars indicate different measuring campaigns.

### 6.4.2. Other Green House Gases

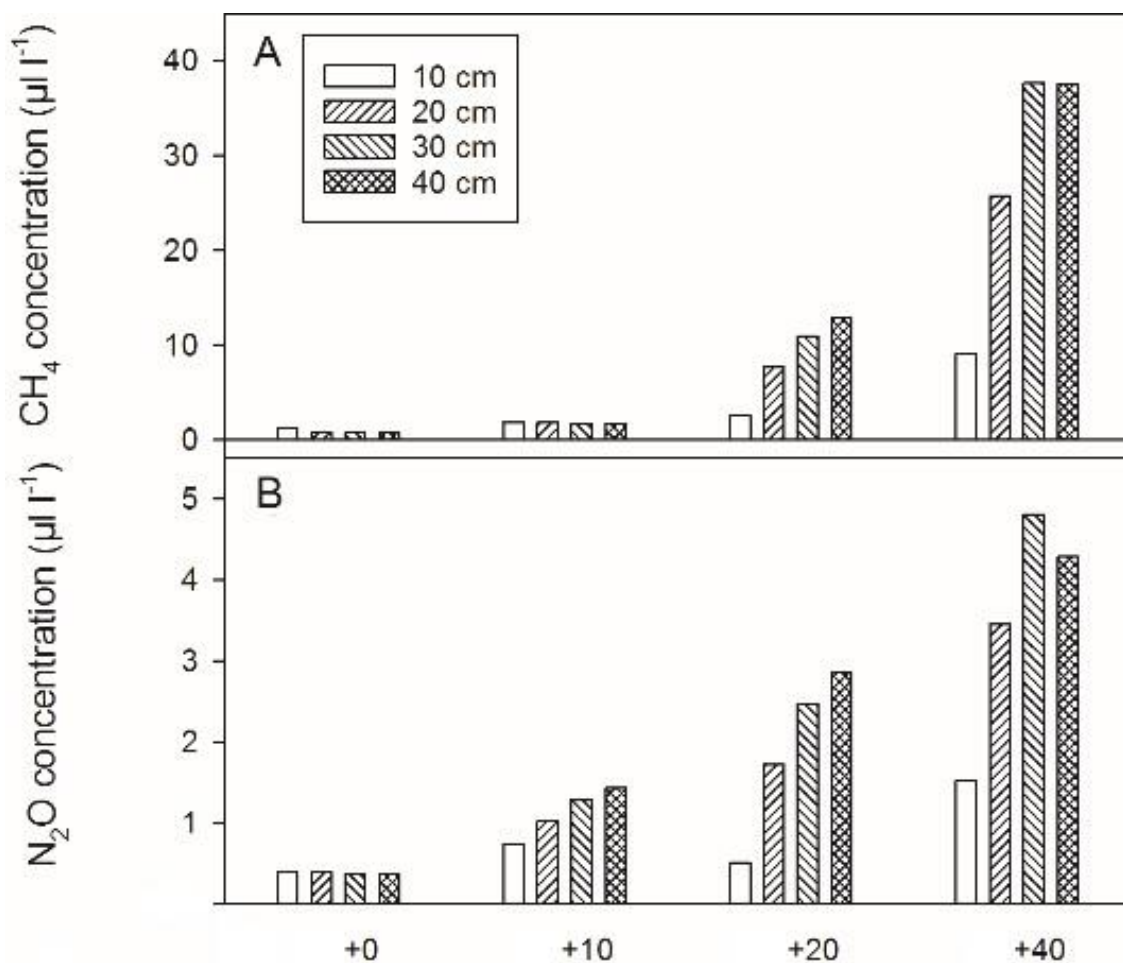
N<sub>2</sub>O and CH<sub>4</sub> fluxes and soil gas concentrations have been measured in two different campaigns (Maljanen, Bhattarai, Biasi, & Sigurdsson, 2018; Maljanen et al., 2017), the latter campaign on both measuring the fluxes in situ and in a laboratory at room temperature (20°C). In the earlier study, that took place in the years 2012-2014, the emissions of N<sub>2</sub>O and CH<sub>4</sub> were measured, and significant differences were found in the flux rates with changing soil temperature from normal ambient temperatures (from 2 to 14°C) up to an elevation of +40 °C (Maljanen et al., 2017). In the later experiment, taking place in July 2016, the former field measurements were repeated and complemented with laboratory studies on the production rates of the gases. Both field measurement campaigns exhibit similar patterns in N<sub>2</sub>O and CH<sub>4</sub> gas fluxes, having similar flux rates at the moderate soil temperatures, and then higher rates beyond the +5°C warming threshold.



**Figure 21.** Measured average field (hatched bars) and laboratory (black and white bars) production rates of CH<sub>4</sub> (A, B) and N<sub>2</sub>O (C, D). Standard deviation (n=3) shown for field measurements, laboratory incubations were made without replicates due to small amount of samples available. The line with triangles down (C) shows the actual soil (10 cm) temperatures in the field and the line with triangles up (B) shows the temperature in the laboratory during gas production measurements. From Maljanen et al. (2018)

*Methane fluxes and soil concentrations*

There was clear CH<sub>4</sub> uptake by the coolest soils (up to +6°C), both in the field and in the laboratory measurements, and the uptake rates were rather similar between field and laboratory measurements, especially for the soils at +10°C. However, the warmest soils had small CH<sub>4</sub> emissions in the field and they did not produce (or consume) any CH<sub>4</sub> in the laboratory experiment (**Figure 21A and B**). The results from the laboratory incubations (Fig. 6.4.2.1 B) may point toward some potential non-biological (geothermal) sources of CH<sub>4</sub>, since laboratory production rates did not mirror the emissions measured in the field. Soil concentrations of CH<sub>4</sub> were between 0.7-1.3 μl l<sup>-1</sup> in the ambient soil temperatures, and decreased with depth, but in the warmer plots concentrations increased with depth up to 38 μl l<sup>-1</sup> (**Figure 22A**).



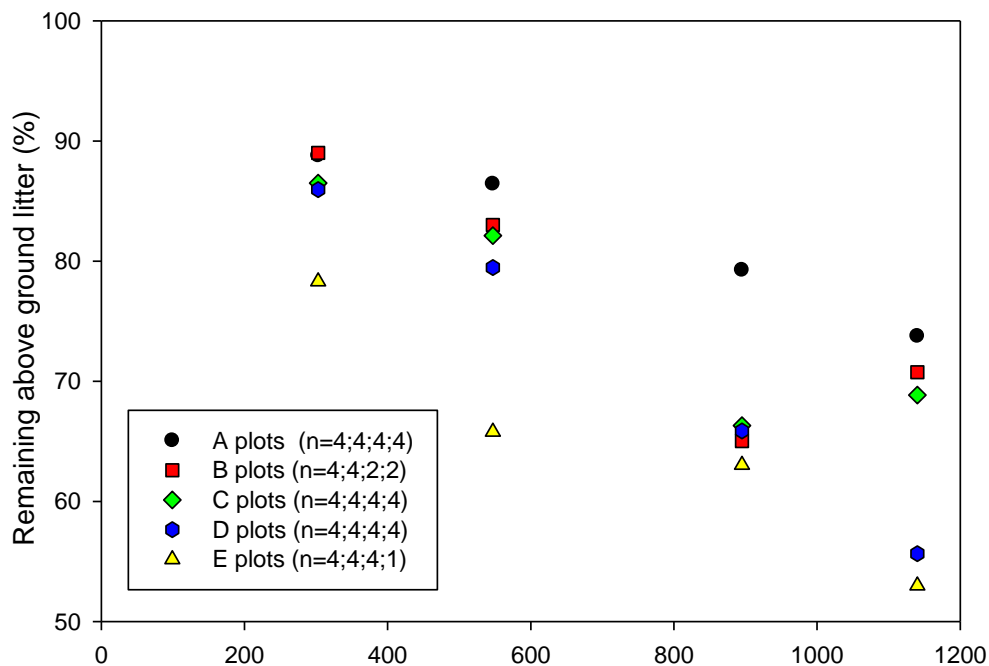
**Figure 22.** Concentrations of CH<sub>4</sub> (A), and N<sub>2</sub>O (B) in soil at depths of 10, 20 30 and 40 cm. Soil temperature at depths of 10 and 20 cm shown in the bottom. From Maljanen et al. (2018)

*Nitrous oxide fluxes and soil concentrations*

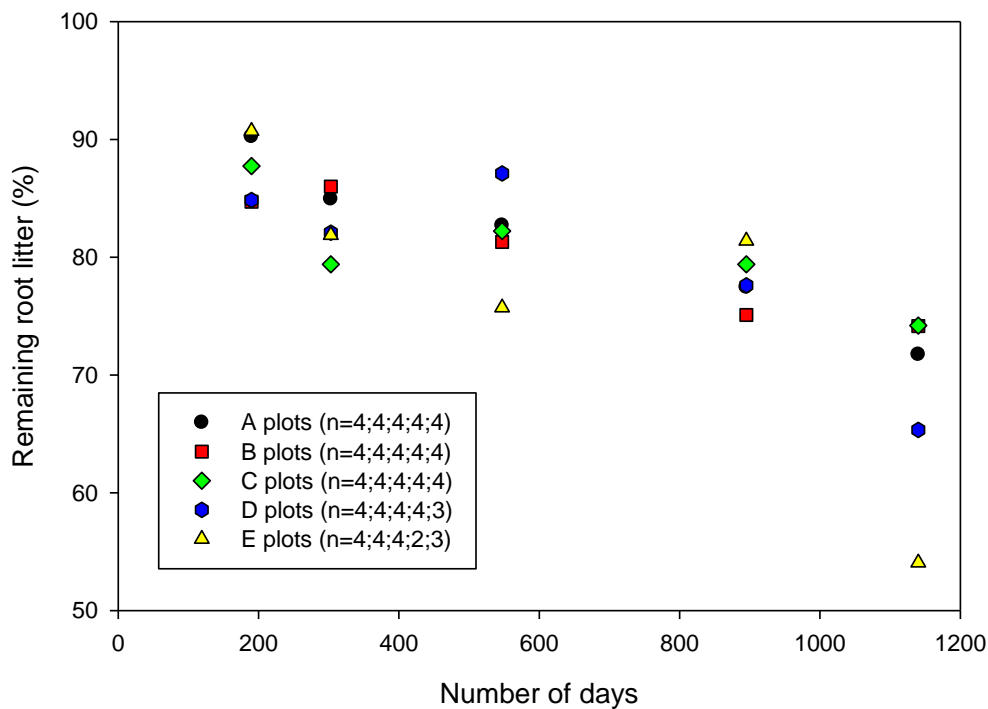
*In situ* measured N<sub>2</sub>O emissions increased with increasing soil temperature ( $p < 0.001$ ,  $r = 0.985$ ). In the laboratory experiment no linear correlation between N<sub>2</sub>O production rates and the original field soil temperature were found. The highest N<sub>2</sub>O production rates were measured from soils at +20°C (depth 0-5 cm) and +10°C (depth 5-10 cm). (**Figure 21 C and D**). Nitrous oxide soil concentrations were from 0.33  $\mu\text{l l}^{-1}$  in the ambient temperature soils (A-levels), and did not differ between depths (10-40 cm). In the warmest plots +40°C, N<sub>2</sub>O concentrations were higher than ambient and increased with depth up to 4.3  $\mu\text{l l}^{-1}$  (**Figure 22B**).

**6.4.3. Litter decomposition**

Litter decomposition is the processes where the litter is broken down by microbes and invertebrates and is converted to humus and part of it leaves the ecosystem as soil respiration (CO<sub>2</sub> efflux). Edda S. Oddsdóttir has studies these C-fluxes by incubating litter bags with a) needle litter (**Figure 23**) and b) fine root litter (**Figure 24**) in litter bags on and in the forest floor in the FN forest. The analysis of this data is under progress, but before decomposition functions can be fitted to the data the samples must be burned for estimating soil contamination.



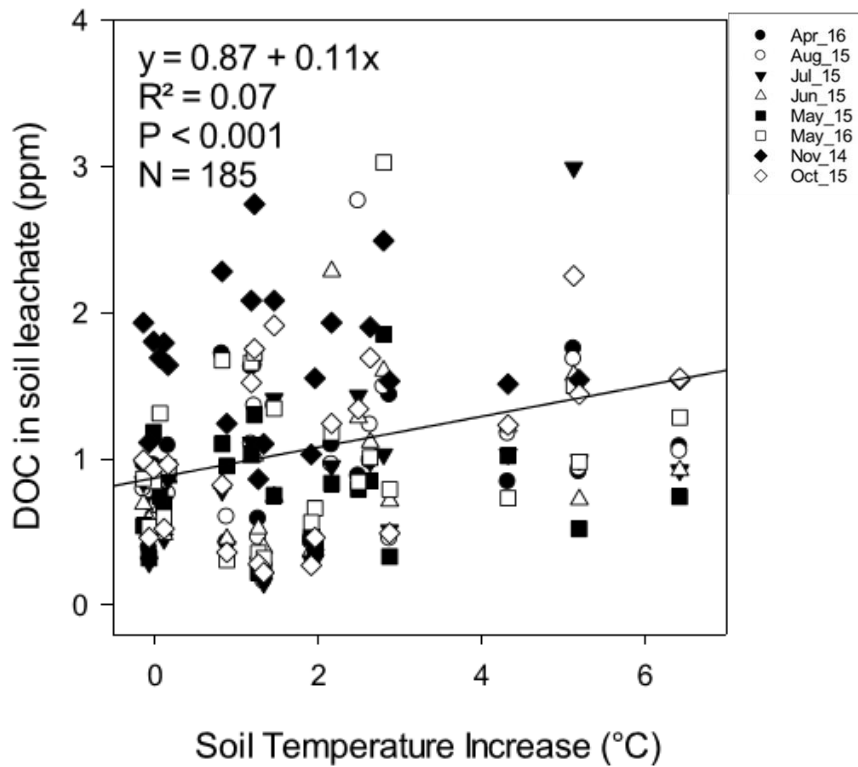
**Figure 23.** Relative loss of needle litter mass during ca. 3 years of incubation (1200 days) at different temperature levels (A-E) in the FN-forest at Reykir. Unpublished data of Edda. S. Oddsdóttir.



**Figure 24.** Relative loss of fine-root litter mass during ca. 3 years of incubation (1200 days) at different temperature levels (A-E) in the FN-forest at Reykir. Unpublished data of Edda. S. Oddsdóttir.

#### 6.4.4. DOC leaching

The flux of dissolved organic carbon (DOC) was estimated by chemically analysing water collected from lysimeters in the forest the seasons of 2014-2016. Warming increased DOC leaching (**Figure 25**; Per Gundersen, 2019, unpublished), probably due to increased decomposition (**Figure 24**).



**Figure 25.** DOC in soil leachate (ppm) according to soil warming level at the water collection site. Data from Gundersen (2019, unpublished).

#### 6.4.5. Soil organic matter

Soil organic carbon (SOC) contents have been measured two times, in soils sampled 2013, and 2017 (**Tables 10** and **11**). It is apparent when those two inventories are compared that there are differences in how they were done. For example, the higher values in the surface layer SOC % in 2013 is likely to be caused by difference in how the litter layer and mineral soil was divided. The differences in the deeper layers (5-20) are less pronounced. Note, that the SOC-percentage in the soil samples from 2017 is still to be corrected by humidity, which might slightly alter the SOC-percentage by <10%.

**Table 10.** SOC-percentage (%) by soil depth and warming gradients, 2013 sampling (N. Leblans & B.D. Sigurdsson, unpublished).

depth	A	B	C	D	E	F
0-5	13.2 ± 1.52	16.1 ± 2.02	15.1 ± 2.13	12.4 ± 1.8	10.2 ± 0.82	n/a
5-10	7.1 ± 0.75	7.6 ± 0.47	7.7 ± 0.61	6.4 ± 0.88	4.7 ± 0.82	n/a
10-20	5 ± 0.53	4.4 ± 0.36	4.2 ± 0.28	4.4 ± 0.35	3.3 ± 0.69	n/a
20-30	4.2 ± 0.83	4.6	3.5	1.8	1.8 ± 0.83	n/a



**Table 11.** SOC-percentage (%) by soil depth and warming gradients, 2017 sampling.

depth	A	B	C	D	E	F
0-5	10.1 ± 0.8	6.9 ± 1.64	10.7 ± 0.97	9.3 ± 1.52	4.6 ± 1.08	4.1 ± 0.47
5-10	10.5 ± 0.7	7.1 ± 0.66	8.7 ± 1.31	6.9 ± 0.61	2.7 ± 0.74	1.8 ± 0.28
10-20	5.1 ± 0.67	4.4 ± 0.48	4.2 ± 0.78	4.8 ± 1.11	2.5 ± 0.74	0.5 ± 0.14
20-30	2.9 ± 0.48	2.3 ± 0.27	4.5 ± 1.64	2.4 ± 0.54	1.9 ± 1.1	0.2 ± 0.13

#### 6.4.6. Soil structure

Soil structure is the three-dimensional arrangement of particles and pore space in the soil. Evaluation of the soil structure was done by determining the poured (or aerated) bulk density of the bulk soil, as well as the coarse (>63 µm) and fine (<63 µm) fractions of the soil (**Table 12**).

**Table 12.** Poured bulk density, coarse (particulate organic matter (POM), SOC in sand and aggregates (SA)) and fine (total silt- and clay-sized SOC (SC) and oxidation resistant silt- and clay-sized SOC (rSOC)) fractions of the soil. From Poeplau et al. (2020, in press).

soil warming gradient	Poured bulk density g/cm <sup>3</sup>	aggregates, 63-2000 µm		fine fraction, < 63 µm	
		POM g C / kg soil	SA g C / kg fraction	SC g C / kg fraction	rSOC g C / kg fraction
Topsoil, 0-10 cm					
A	0.53±0.02	11.8±2.6ab	6.8±0.5a	5.1±0.2a	1.6±0.1a
B	0.54±0.04	21.6±4.4a	6.3±0.7a	4.9±0.3a	1.6±0.1a
C	0.57±0.03	12.9±1.8abc	7.1±1.0a	5.4±0.2a	1.9±0.1a
D	0.58±0.03	16.0±3.5ab	5.8±0.4a	5.2±0.1a	1.7±0.1a
E	0.67±0.02	6.0±1.5bc	5.2±0.6a	5.0±0.3a	1.8±0.1a
F	0.78±0.02	0.4±2.6c	2.6±0.4b	3.3±0.2b	1.1±0.1b
Subsoil, 20-30 cm					
A	0.72±0.03	3.4±0.8a	2.9±0.7a	4.1±0.3a	1.3±0.1a
B	0.75±0.02	3.4±0.7a	1.7±0.4ab	3.8±0.3a	1.4±0.2a
C	0.76±0.02	2.0±0.3ab	1.5±0.4ab	3.8±0.5a	1.2±0.2a
D	0.77±0.01	2.1±0.7ab	1.2±0.1ab	3.4±0.2a	1.1±0.1a
E	0.80±0.03	0.8±0.2b	0.9±0.2b	3.1±0.4a	1.1±0.2a
F	0.91±0.01	0.3±0.1b	0.2±0.0c	0.5±0.2b	0.2±0.1b

#### 6.4.7. Other measurements

Soil pH was measured in July 2016, and varied between 5.4. and 6.7, having no clear correlation with temperature; however, the highest pH was measured from the warmest +40°C plot at a depth of 5-10 cm (Maljanen et al., 2018).

## 6.5. WP IV: The mortality of the present coniferous trees and their displacement by deciduous ones

The fourth research question is: (IV) to quantify and study the dieback of the coniferous trees along the warming gradient, and their replacement by deciduous woody species during the first decade after the warming started. Why do the conifers die off in warmer soils but deciduous seedlings can establish there instead?

As visible on Fig. 1b) the spruce trees have died off at a certain soil temperature limit (+15°C mean annual temperature or so), and the species transition into deciduous takes place around that temperature limit or before.

The growth decline of the spruces and the emerging of deciduous woody species is documented in the inventory measurements of the 50 m<sup>3</sup> plots, carried out between every vegetation period and still ongoing. In the inventory, the transition is reflected as taxational diameters and heights of the trees, and only the forest with the lower temperatures of the gradient (up to the spruce total mortality) are measured. The transition itself has been quantified, as a relative foliage coverage and taxational measures of the woody vegetation, during the summers 2017 and 2018, as well as the species composition of the deciduous trees (Bischof, 2017; Wisniewski, 2018).

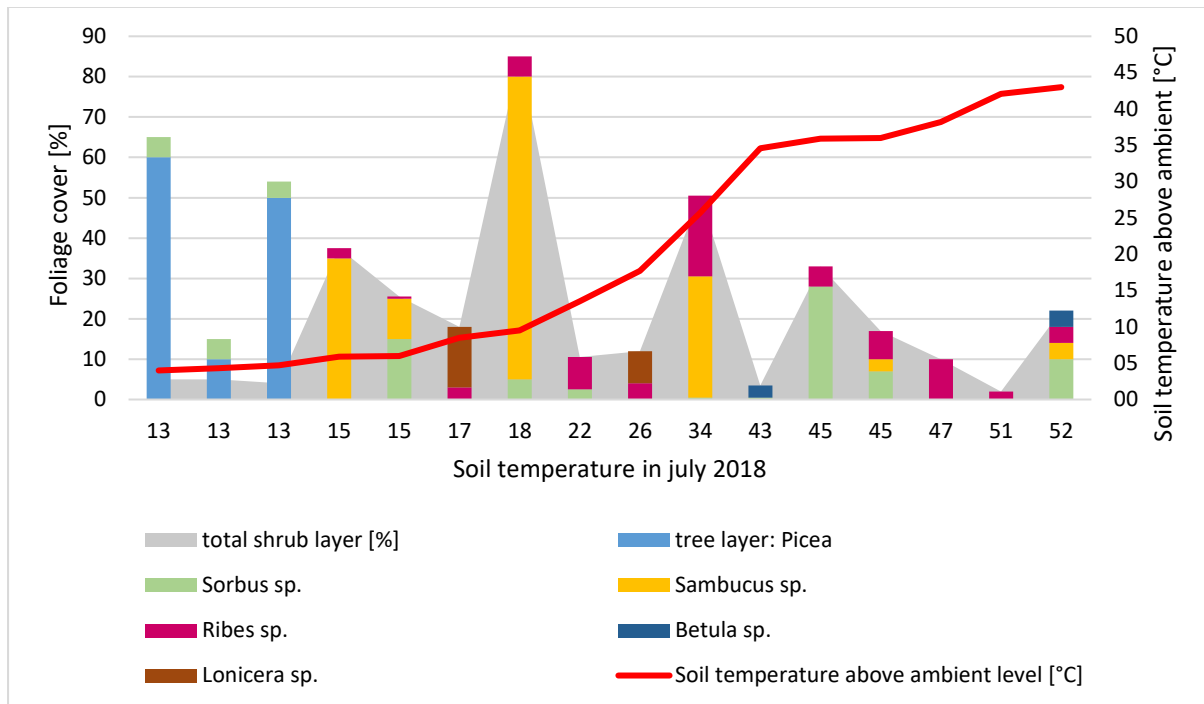
### 6.5.1. Mapping of temperature changes

An independent gridline has been set up in the forest, ranging from outside the forest area in the ambient soil temperature, and covering the soil warmed forest as well as the hottest soil area, which makes it easy to make point measurements of the soil temperature when desired. It has been noted (Maljanen et al., 2018), that the highest soil temperatures are less spatially stable than the moderate soil warming levels. The warming gradient is also more steep in the higher (>10°C) range of soil warming (see fig. 1a).

### 6.5.2. Vegetation succession

The species composition and relative foliage coverage according to the soil temperature, was recorded in July 2017 (**Figure 26**; (Bischof, 2017)). As there are no continuous soil temperature measurements outside the permanent plots, the soil temperature was measured three times during two weeks, thus giving the relative soil temperature in each plot. When the woody vegetation was characterized as foliage cover (where 100% is a full, single layer cover, and 0% is no green woody vegetation), the transition in woody vegetation was clear (**Figure 26**). The coniferous spruces disappeared where the temperature was more than +7-10 °C over ambient. Instead the deciduous woody vegetation, which consisted of various unidentified species of the genera of *Sorbus* spp., *Ribes* spp. and *Lonicera* spp., as well as abundantly growing *Sambucus* spp. successfully colonized these warm areas. These species of shrubs are all brought by birds. Interestingly, some occasional individuals of the Icelandic downy birch (*Betula pubescens*) were also recorded as successful colonizers within the warmer areas, where the conifers could not survive.

As shown on **Figure 26** the *Sambucus* spp. is the most abundant shrub species in the intermediate warmed soil, but becomes less frequent in the more warmed soil. It is to be noted, that *Sambucus* spp., where present, has a habitus of many stems and broad foliage, and that is reflected in the high foliage cover percentage.



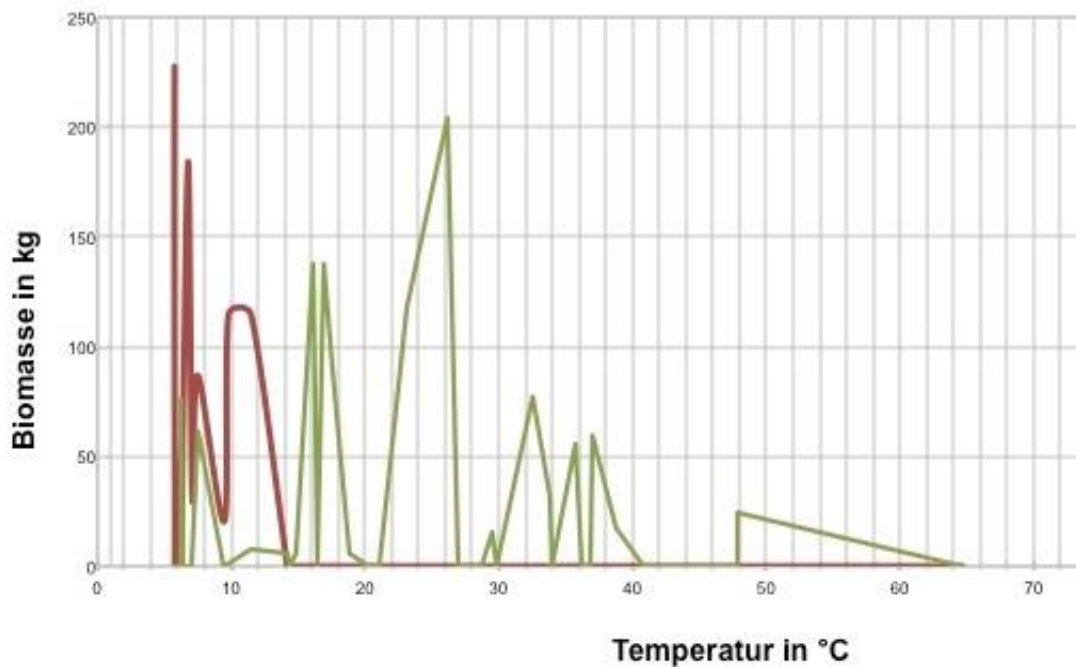
**Figure 26.** Foliage cover of spruce and shrub genera according to soil temperature in July 2017.

Another survey was done during the summer 2018 (**Figure 27**, (Wisniewski, 2018), with an emphasis on the biomass of the woody vegetation, and with a more dense gridline of plots. All the trees in a 3,14 m<sup>2</sup> round plot were measured, and Icelandic biomass equations (Snorrason & Einarsson, 2006) used to calculate biomass for the spruce, and a general biomass equation from Germany used for understory woody vegetation (Wolff et al., 2009).

It is obviously incorrect to use one formula for all the shrubs, and using a formula based on German inputs could lead to an overestimation of the present shrub vegetation. Any comparison of the spruce and shrubs is limited to the age difference, the spruces being >50 years old, but the shrubs not more than 10 years. However, it gives a useful view of the situation, showing the same patterns as the foliage cover estimation: a clear disappearance of the spruce around 13°C (~7,5°C MAT) and shrubs growing abundantly under the soil temperatures 10...35°C (~7-25°C MAT) (**Figure 27** and **28**).

A disadvantage of the dieback study site is that it is relatively small, or less than 1000 m<sup>2</sup> (**Figure 1** and **28**), i.e. the area where the spruce dominated vegetation has converted into shrub dominated vegetation. Succession is a phenomena consisting of changes in quantities

of individuals, and thus needs a considerable number of individuals to be characterized sufficiently. Therefore, it might prove difficult to publish those findings in an international journal, however interesting the findings are.



**Figure 27.** Biomass of the woody vegetation in accordance to the soil temperature in July 2018. Brown – spruce (kg/ 10 m<sup>2</sup>); green – shrubs (kg/ha). Note that the shrub vegetation is multiplied 1000-fold to the spruce, for visualization.

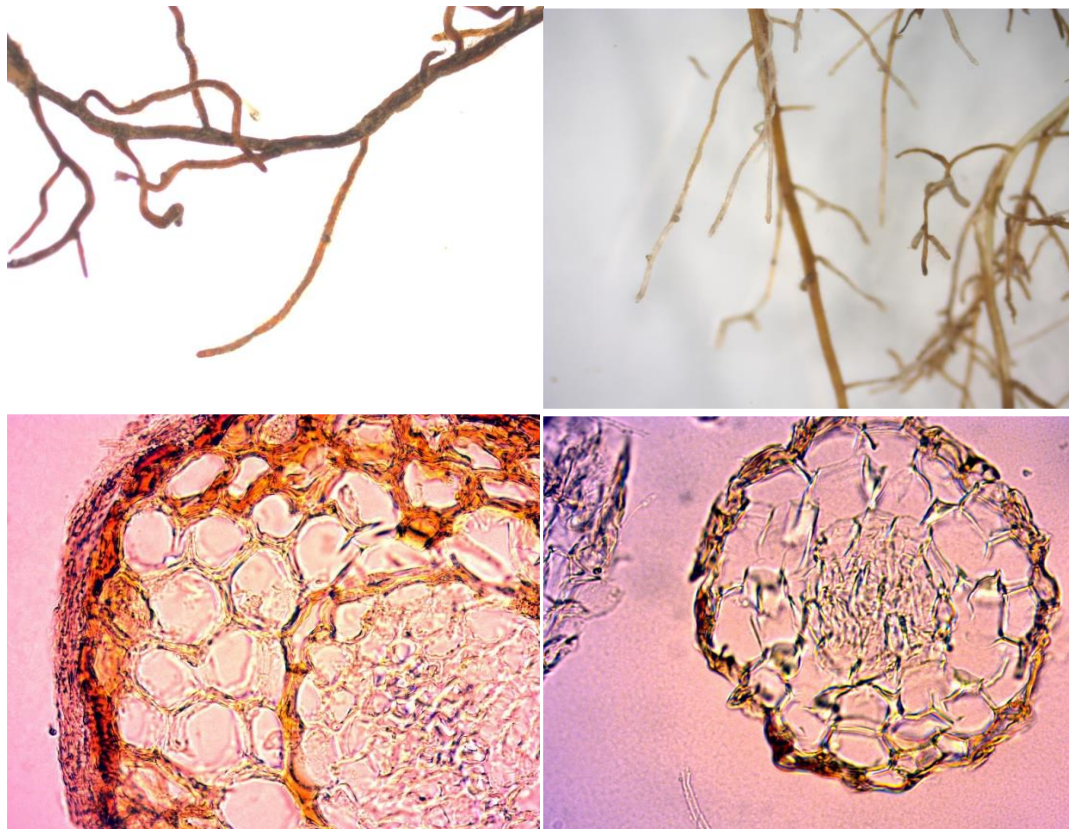


**Figure 28.** Student Ben-Lukas Wisniewski standing in the warmer soil area.



### 6.5.3. Other measurements

It has been observed that the roots of the woody vegetation in the warmest soils grow only at the soil surface, and have visibly different anatomy from normal fine roots in the forest. Samples were taken from roots of a small spruce tree growing where any middle aged spruce was already dead, as well as from a birch tree growing in the warmer soil (**Figure 29**). No systematised research has though been done on these, but it might be interesting in the future.



**Figure 29.** Anatomy of fine roots at high soil temperatures. Upper – macroscopic image of fine roots. Lower – internal anatomy, cross section. Left side – spruce, at a temperature, approximately  $+15^{\circ}\text{C}$  above ambient. Right side – birch, at a temperature, approximately  $+25^{\circ}\text{C}$  above ambient. Images from Ivika Ostonen.

## 7. Conclusions and current state of knowledge and future plans

As described in the present report, various parameters of the forest ecosystem have been measured along the soil warming gradient. These parameters respond differently to the soil warming – but in general the growth and C-stock of the above-ground part of the trees responds positively to the warming up to +3°C, but after that negatively, as seen in the patterns of LAI and stem volume. The photosynthetic measurements show the same trend – the decrease in photosynthetic activity appears only above +3°C.

Further:

- Soil parameters, such as SOC content and SOC in aggregates, respond clearly to the soil warming around +5°C.
- The belowground response is more clear right from ambient: the fine root biomass is lower, and the root longevity decreases already when the warming is +3°C.
- Surprisingly the soil warming also affects the aboveground growth phenology. At the soil warming level of +7°C the shoots start and finish growth earlier, but the difference between ambient and +3°C is less pronounced.
- The belowground phenology, i.e. the fine root phenology, is a matter of ongoing research, but very interesting.



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## 9. Appendices

Here is one published article and two manuscripts that will become part of Páll Sigurðsson's PhD thesis

**Appendix 9.1** Christopher Poeplau, Páll Sigurðsson, Bjarni D Sigurðsson (20XX). Strong warming of a subarctic Andosol depleted soil carbon and aggregation under forest and grassland cover. Submitted to *Soil*

**Appendix 9.2** Páll Sigurðsson, Ivika Ostonen, Edda S. Oddsdóttir, Bjarni D. Sigurdsson (20XX). Soil warming effects on fine-root turnover in a mature Sitka-spruce forest in southern Iceland. (in preb).