Long-term acclimation to soil moisture alters sensitivity to sudden summer drought in Norway spruce

Investigating site dependent soil moisture acclimation as a factor in carbon assimilation in drought stressed Norway Spruce (*Picea abies*) in South-West Sweden

Esther Lutz

Degree project • 30 credits
Swedish University of Agricultural Sciences, SLU
Southern Swedish Research Centre
Euroforester Programme
Alnarp 2026

People I would like to thank

I have many people to thank for their support with this project, but owe special thanks to:

Dr. Leonie Schönbeck, for the endless patience and thorough feedback, for involving me in excursions and your project and for teaching me everything about Ecophys I know. Thank you also for the advice, damage- and quality control and for letting me name your osmometer “Ozzy”. Hartelijk dank voor uw steun tijdens en na dit project; ik waardeer het enorm.

Dr. Maartje Klapwijk for sharing your data and your project. It has been a lot of fun working with you.
Dr. Petra Fransson, also for sharing your data and the impromptu crash course in mycology.

Stort tack till hela gänget i Tönnersjöheden för stödet med fältarbetet – både för uppsatsen och under sommaren. Thank you, Dr. Martin Goude, for the support, patient advice on my research idea word-salads and unintentionally improving my site finding skills.

Till Erik. Tack älskling för tålamodet, björnkramarna, litrarna av te och kaffe och dina försök att lista ut mina fel i R. Tyvärr gillar jag verkligen forskningsämnet så...encore?

Long-term acclimation to soil moisture alters sensitivity to sudden summer drought in Norway spruce – Investigating site dependent soil moisture acclimation as a factor in carbon assimilation in drought stressed Norway Spruce (*Picea Abies*) in South-West Sweden

Långsiktig acklimatisering till markfuktighet förändrar granens känslighet mot plötslig torrhet under sommaren – Undersökning av acklimatisering till ståndortbaserad fuktighet som faktor i kolassimilering i torrhetsstressade gran i sydvästra Sverige

Esther Lutz

Supervisor:	**Leonie Schönbeck, PhD, Swedish University of Agricultural Sciences, Southern Swedish Forest Research Institute**
Examiner:	Amanda de Castro-Segtowich, PhD, Swedish University of Agricultural Sciences, Southern Swedish Forest Research Institute

Credits:	30 credits
Level:	A2E
Course title:	Master’s thesis in Forestry Sciences
Course code:	EX1034
Programme/education:	Euroforester (MSc) - SM008
Course coordinating dept:	Southern Swedish Forest Research Centre
Place of publication:	Campus Alnarp
Year of publication:	2026
Copyright:	All featured images are used with permission from the copyright owner.
Keywords:	drought, turgor loss point, site acclimation, carbon assimilation

Swedish University of Agricultural Sciences
Faculty of Forestry Sciences
Southern Swedish Forest Research Centre

Abstract

The aim of this thesis was to reveal the impact of long-term acclimation to soil moisture conditions, induced by site elevation, on the physiological and morphological drought response of Norway spruce. A rain exclusion experiment was set up in a Norway spruce forest with understory roofs, excluding 100% of precipitation. The roofs were built on either higher (xeric) or lower (mesic) sites within the stand, characterized by lower and higher soil moisture, respectively. Gas exchange (assimilation A, stomatal conductance to water vapor g_{sw}, intrinsic water use efficiency iWUE) measurements were taken in three separate field champagnes spanning June 2025 to April 2026, and combined with ψ_{Stem} data, turgor loss point π_{tlp} and needle morphology data (Shoot length, needle length, specific leaf area) to analyse drought response. No evidence of a morphological drought acclimation response could be found in the needles and shoots, neither in response to long-term (site condition) or short-term extreme drought (roof). Similarly, no physiological acclimation of the turgor loss point as a reaction to the drought simulation could be measured after one year.

However, short-term physiological drought response of gas exchange showed a significant difference between xeric and mesic sites: photosynthesis of trees on the xeric site was more negatively affected by roofs than trees on the mesic sites, during June. The control trees on the xeric sites could maintain high levels of photosynthesis and stomatal conductance. This indicates that xeric acclimated trees could uphold photosynthetic activity during the drier summer months, but the treatment pushed them into drought stress. Autumn was characterized by an overall quick recovery of gas exchange. These results lead to the conclusion, that a long-term site acclimation of photosynthetic sensitivity is present, but subject to seasonal variations.

Keywords: drought, turgor loss point, site acclimation, carbon assimilation, Norway Spruce

Table of contents

List of tables

List of figures

Abbreviations

Abbreviation	Description
DBH	Diameter at Breast Height
EU	European Union
g_{sw}	Stomatal Conductance to Water Vapor
HR	Hydraulic redistribution
LULUCF	Land-Use, Land-use change and Forestry
TLP	Turgor Loss Point
SLA	Specific Leaf Area
SLU	Swedish University of Agricultural Sciences
VPD	Vapor Pressure Deficit
iWUE	Intrinsic Water Use Efficiency
WUE	Water Use Efficiency

1. Introduction

As anthropogenic climate change progresses, forests and forestry are increasingly viewed as a last feasible resort of climate change mitigation by policy makers. For example, under the EU's LULUCF (Land Use, Land-Use Change Forestry) regulation, Sweden and Germany are intended to host the largest forest carbon sink in the European Union by far, with decreasingly sized carbon sink targets for every EU member state by 2030 and 2050 respectively (Commission, Reg. 2023/839, European Commission, 2023). The overarching aim behind efforts to increase Europe's terrestrial carbon sink's capacity, is to afford climate action in other sectors more time for upscaling (Naturvårdsverket, 2026). However, both Sweden and Germany currently lag behind their targets (Bundeswirtschaftsminsterium, 2022; Naturvårdsverket, 2025a) due to, among other factors, severe summer droughts slowing tree growth and subsequent recovery (Bundesministerium für Ernährung und Landwirtschaft, 2022; Naturvårdsverket, 2025a).

Current carbon sink assessment under the LULUCF regulation, however, has limited spatial sensitivity and is not fully taking the impact of long-term site conditions into account (Naturvårdsverket, 2025b), as these may influence tree's resilience to water stress and thus carbon sequestration during droughts. This is especially relevant for the economically important Norway Spruce (*Picea abies* (L.) H. Karst.), which has been found to be more vulnerable to drought than Scots Pine (*Pinus sylvestris*) or Birch (*Betula* spp.) (e.g. Lagergren & Lindroth, 2002; Gutierrez Lopez et al., 2021; Aldea et al., 2023), due to its shallow root system.

Norway Spruce is native to most of Sweden and constitutes circa 38% of the total growing stock in Swedish forest (Wikberg, 2023). It is a relatively fast growing species and coupled with its relatively uniform shape, rotation periods of 60 to 105 years, established seedling industry, high shade tolerance, self-pruning and relatively low browsing pressure (Skogforsk, 2026), Norway Spruce is a competitive species on most soils. For ease of management, Norway Spruce is often planted in monoculture or mixed stands with Pine. Consequentially, much of Sweden's tree nursery and sawmill industry as well as its timber product export is based on an increasingly climate sensitive species (Schulte et al., 2026) .

Water is at the root of everything – core physiological processes and acclimation

The availability of water to the roots is essential, because trees are subject to transpiration from their stomata, via the root and stem xylem (Khadke et al., 2026). This transpiration is mostly driven by the atmospheric transpiratory demand (vapor pressure deficit, VPD), which depends on both temperature and relative humidity (Grossnickle, 2000; Busch et al., 2024). Essentially, a pull-effect from areas of high water potential ψ in the soil to more negative water potential ψ in the tree, i.e. the needles, is created, the soil-plant-air continuum (SPAC). Water potential is expressed as energy per unit volume and can be understood as the energy status of water within a plant (Richter, 1978; Grossnickle, 2000).

The more energy required to pull water from soil to needles and the more negative plant ψ , the more drought-stressed a tree becomes. Under favourable growing conditions, the water potential ψ in a tree is more or less 0, balancing the positive turgor pressure potential (ψ_p) with the negative osmotic potential (ψ_π) (Richter, 1978; Richter & Kikuta, 2014). Here, the former can be understood as the water pressure maintaining a cell's functional shape and the latter the concentration of solutes, such as carbohydrates, in a cell. If cell turgor pressure potential declines to 0, turgor loss point (π_{LTP}) is reached, which becomes visible as wilting.

The flow of water along the SPAC fills a vital plant function. During photosynthesis (*A*), CO_2 diffuses through the stomata while water vapor evaporates, forming an important upward trajectory of water and nutrients (Farquhar et al. 1980). Through stomata opening, commonly described as stomatal conductance to water vapor (g_{sw}) (Kaiser & Paoletti, 2014; Busch et al., 2024) the tree regulates transpiration and carbon assimilation. Changes in stomatal conductance are fuelled by the interaction between soil water availability and atmospheric evaporative demand, thus affecting gas exchange and photosynthesis. The physiological aspects of stomatal conductance further influence a trees intrinsic water use efficiency (iWUE), a ratio between assimilation rate A and stomatal conductance (g_{sw}), which describes how much carbon a plant or tree gained per unit of released water (Busch et al., 2024).

There is evidence that acclimation to predisposing conditions, such as long-term soil water availability, influence both the physiological and morphological drought response of trees, so that estimates of carbon sequestration become less accurate, leading to more insecurity about carbon sink potential of the forest.

Gessler & Zweifel (2024) describe trees to be in a constant re-evaluation state on how to best allocate resources, based on recent changes in the environmental conditions, and the changes in functional and structural traits undergone previously. Changes in functional traits include stomata closure or photosynthesis and can happen within minutes to a few weeks, depending on acclimation. For example, when comparing hydrological processes of Norway Spruce on high, medium and low soil moisture sites in southern Finland, Ge et al. (2011) noticed a rapid and earlier decline of canopy conductance at the low soil moisture site compared to the other sites, indicating an acclimation to drought at stomatal level.

Structural changes in turn tend to happen within weeks or months or with the delay of several years, depending strongly on acclimation and to a lesser degree of the lifespan of the affected tree (Gessler & Zweifel, 2024). One example of structural change in reaction to sustained drought stress is the decrease in crown size to reduce the overall leaf area and thus evaporative potential (Zhu et al. ,2022). This can occur by shedding part of leaves or needles, but also by reducing the size of leaves, often reducing the specific leaf area (SLA), the ratio of needle surface to dry weight. This functional trait is a commonly used indicator for resource availability (Busch et al., 2024).

However, structural acclimation, such as a smaller leaf area, can affect other functional traits, e.g. decrease in photosynthetic activity due to a lower amount of stomata, even after the drought stress has receded (Hesse et al., 2024), the so called *drought legacy effects*. For example, ecophysiological research on Scots Pine experiencing sudden prolonged drought stress shows, that those trees experiencing no previous water shortage only exhibited a decrease in gas exchange three years after onset of drought (Schönbeck et al., 2022). Similarly, Hikino et al. (2025) observed a delay in leaf area recovery in a mature mixed spruce and beech (*Fagus sylvatica*) stand recovering from the same drought treatment, where spruce still displayed 30% leaf area reduction four years after drought release and beech showed no significant difference in leaf area. However, the same authors found that spruce with a drought legacy effect could maintain higher leaf gas exchange and sap flow density levels during a subsequent drought than the control group (Hikino et al., 2025), illustrating the interaction of structural and functional trait acclimation over time.

As climate change accelerates, soil water availability may become an increasingly limiting factor to photosynthesis, and thus growth, but at different speeds and with different impacts at different sites (Ogana, 2024, Goude, 2022). Ecophysiological research into site acclimation as a factor in species-specific responses to drought can therefore contribute prospectively towards an increased accuracy of carbon sink estimates and climate change adapted regeneration practices.

1.1 Aim, objectives and scope of thesis

The aim of the thesis is to reveal the impact of long-term acclimation on the physiological and morphological drought response of Norway spruce.

A field manipulation experiment, with roofs placed around trees growing in xeric and mesic growing conditions in the same stand, inducing drought by decreasing the amount of precipitation reaching the forest ground, was used to reach the following objectives.

To fulfil the aim, the first objective of this thesis is to test whether the long-term exposure to xeric or mesic growing conditions resulted in morphological (needle morphology) and drought tolerance (needle turgor loss point) acclimation in the trees.

The second objective is to establish whether long-term acclimation to xeric or mesic growing conditions affects the physiological drought response (gas exchange, stem water potential) of the trees.

1.1.1 Working hypotheses

The following working hypotheses are stated:

H_1: Trees acclimated to long-term xeric conditions have reduced sensitivity of stomates to sudden drought, resulting in higher levels of photosynthetic activity under drought compared to trees acclimated to mesic conditions.

H_2: Physiological acclimation (e.g. needle turgor loss point, stomatal closure) in Norway spruce occurs both in response to long-term and short-term soil moisture changes. Turgor loss point is expected to be lower in xeric conditions and in response to short-term drought.

H_3: Long-term acclimation to soil moisture results in smaller needles with a lower specific leaf area, while one growing season of drought did not yet affect needle morphology.

1.1.2 Structure of thesis

The following Chapter 2 first describes the experimental site and experiment set up, followed by the methods employed in data collection. The chapter ends with a description of the statistical analysis.

In Chapter 3, the focus is on presenting the results for data gathered in 2025 and spring 2026, with particular attention paid to treatment effects and effects of growing conditions during these years as well as any differences between them. Thereafter, Chapter 4 discusses these results in relation to the hypotheses, as well as and their limits in context to the literature and aims to establish whether the working hypotheses can be accepted. Conclusions and an outlook for further research can be found in Chapter 5 and a popular science summary in Chapter 6.

2. Methods

2.1 Study site and species

Norway Spruce (*Picea abies (L.) H. Karst*.), is a native, shade tolerant conifer, which thrives on fertile to moderately fertile and relatively moist soils where it can outcompete Scots Pine (*Pinus sylvestris)* in terms of volume growth (Skogforsk 2026).

Drier or clay-rich soils can limit its growth or weaken the shallow rooting Norway Spruce, which increases its susceptibility towards pests and pathogens. Two of the most common pests are root rot (*Heterobasidion annosum*) and bark beetle attacks (*Ips topographus)*, but spring or summer frosts, wind felling and increasingly warmer temperatures and drought cause damage as well (Ogana et al., 2024; Skogforsk, 2026).

Tönnersjöheden research park is located just outside Simlångsdalen, east of Halmstad in the county of Halland at the Swedish West coast (see Figure 1).

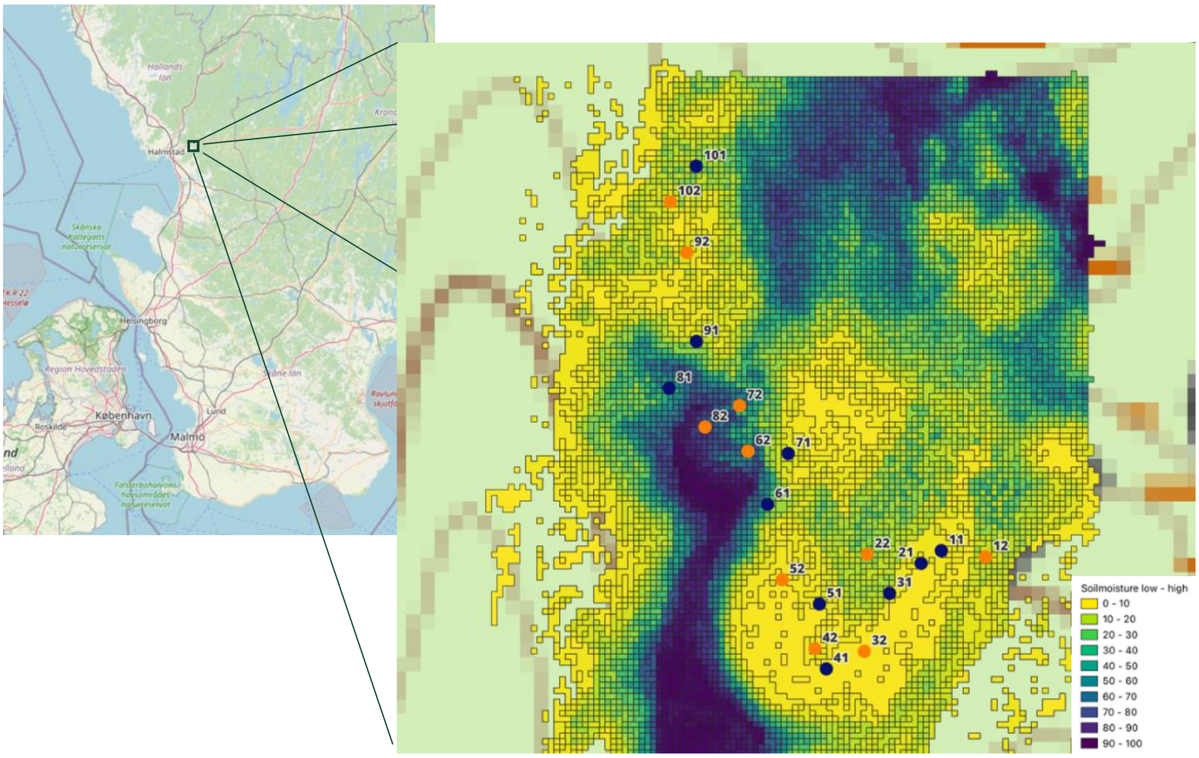

Figure 1 *Left: Map of the location of Experiment #8280 in Tönnersjöheden Försökspark in Halland. (Silvaboreal - Försök 8280, n.d.) Right: Detailed map of the experimental site "Eriksköp" including modelled soil moisture from wet (dark blue) to dry (yellow) and all target trees. Map curtesy of Dr. Maartje Klapwijk, Department of Ecology, SLU Uppsala.*

The research park experiences a maritime climate, with average annual temperatures of 6.9°C and a mean annual precipitation of 1050mm (SLU Tönnersjöheden, 2025). Temperatures during the study period (April 2025 to April 2026) fluctuated between -19,1°C and 30°C, with an average of 8.48 °C over the whole year of 2025 (see Figure 2). The average temperature during the first four months of 2026 was -0.5°C, with the lowest temperatures of -19.1°C measured in mid-February. Total precipitation for the study period amounted to 470.1mm , excluding precipitation in form of snowfall.

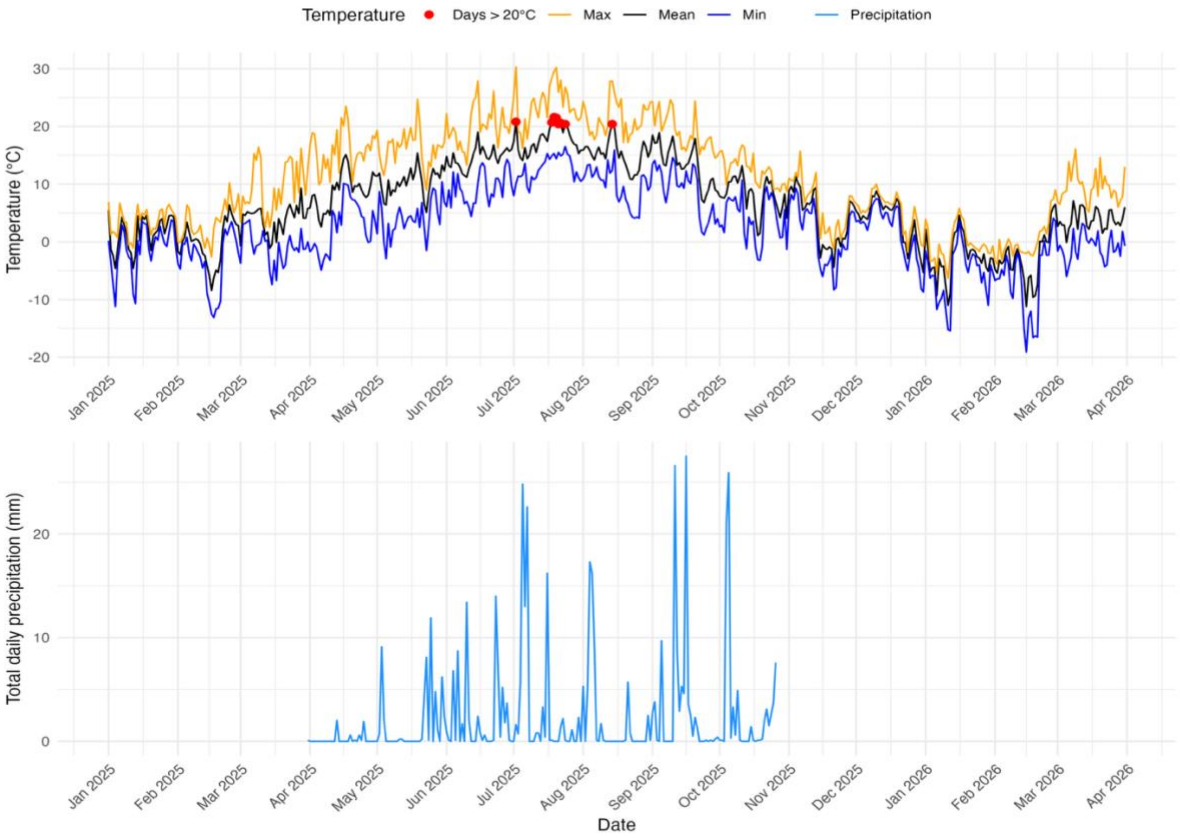

Figure 2 *a) Daily temperature mean, maximum and minimum at Tönnersjöheden's climate station, recorded from April 1st, 2025, to April 30th 2026.b) Daily total precipitation for April 1st, 2025, to April 30th, 2026, at Tönnersjöheden research station. Weather Data provided by the Unit for Field-based Forest Research, SLU in accordance with standard WMO protocols. (Anon 2026).*

All data stems from one drought simulation site "Eriksköp site" just outside the Eriksköp Nature Reserve (Silvaboreal #8280). The site is dominated by planted Norway Spruce aged ~40 years, with an understory of different mosses and blueberry (*Vaccinium myrtillius*) shrubs. The surrounding, non-commercially used forests are dominated by European Beech (*Fagus sylvatica*) mixed with other broadleaf species.

While the regional landform is described as moraine with an undulating topography and a groundwater table at more than 2m depth, this groundwater table varies with seasons and is influenced by the high soil permeability, due to stoniness, sandy texture and overall good drainage (Sommer, 2024). The decisive soil formation process across all microsites was classified as podsolation, with an available field capacity estimation of 13% to 15% (low) and a pH-value range of 5 (lower Site) and 4.5 (upper Site), indicating a very poor nutrient status (Sommer, 2024).

The soil at Eriksköp site was analysed at two distinct areas within the site in terms of elevation and modelled soil moisture (upper and lower site) prior to the installation of the treatment roofs in autumn 2024, due to the topographical heterogeneity at Eriksköp site. The soil assessment report highlights the poor access to water at the upper site, due to its location at the top of a moraine (Sommer, 2024). However, there were and are sections at the microsite lower site with visible standing water after rainfalls.

In the following sections of this thesis, lower site will be referred to as 'mesic site' and Upper Site as 'xeric site'. A difference in mean DBH can be observed between these two elevation levels, where trees on the xeric site had lower DBH than those on the mesic site before the installation of the treatment roofs in 2024 (Table 1).

Table 1 Overview of DBH of all target trees in Eriksköp by site elevation in 2024.

Mesic		Xeric	
Tree No	DBH	Tree No	DBH
61	30.2 cm	11	24.7 cm
62	24.6 cm	12	30.1 cm
71	27.3 cm	21	30.4 cm
72	29 cm	22	26 cm
81	32 cm	31	31 cm
82	32.2 cm	32	24.3 cm
91	32.5 cm	41	24.1 cm
92	26.5 cm	42	30,5 cm
101	32.5 cm	51	26 cm
102	29.3 cm	52	31.5
Mean	29.6 cm	Mean	27.86 cm

2.2 Experimental design

This thesis is based on data from a larger, long-term experiment simulating drought-stress and bark-beetle attack responses. Key structure of this experiment are 10 translucent subcanopy roofs, located at 1,5 to 2m above ground (Figure 3). The experiment is duplicated in a nearby stand with comparable species composition and elevation, but measurements for this thesis were concentrated to only one site. The construction of these roofs was finished in early Spring 2025 before budburst and the roofs will remain installed for at least four years. At each experimental site roofs are built around a central ‘target tree’, while including two to three additional individuals (Figure 3, left picture). Each target tree is paired with a control tree nearby.

The roofs have a 100% coverage, with the aim to simulate a near complete stop of precipitation throughfall during this period. To achieve this, pool tarp was installed at the meeting point of target tree and roof to close-off any throughfall. (Figure 3, right picture).

Temperature and precipitation during the experimental period for this thesis (April 2025 to April 2026, see Figure 2) are measured at the climate station at Tönnersjöheden’s försökspark, as this is the nearest meteorological station to the site. Soil water content sensors are installed at 20 cm depth approximately 1 m from the target tree stem, logging every 15 minutes (% Volumetric Water Content, VWC).

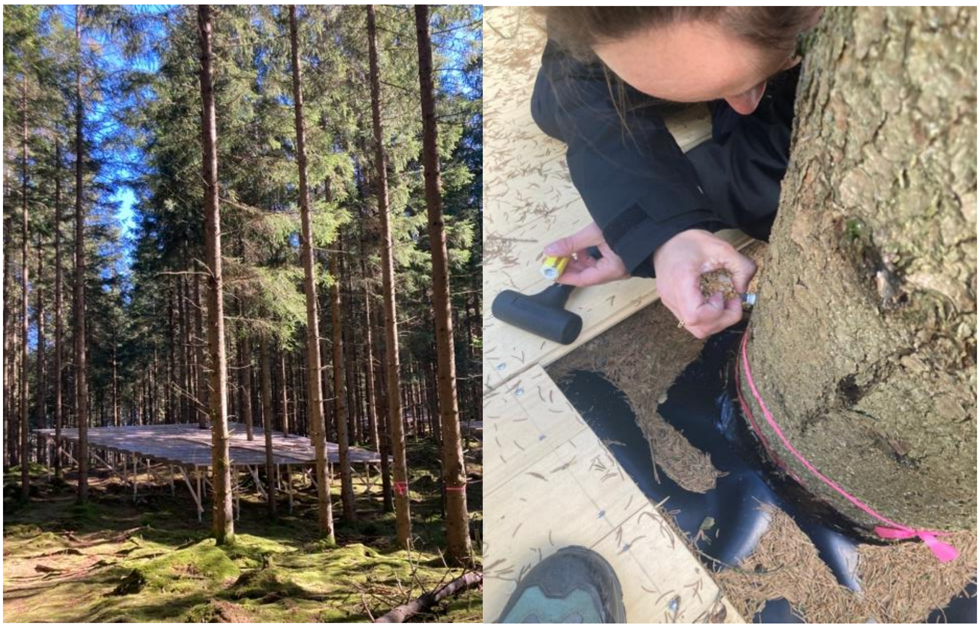

Figure 3 *Left: Drought simulation roofs at Tönnersjöheden. Picture taken in Spring 2025. Right: Target tree with pool tarp covering the gap to the roof. Picture taken in April 2025 during Dr. Schönbeck’s installation of FloraPulse sensors. Student’s own.*

2.3 Sampling and measurements

Before the onset of this MSc thesis, physiological measurement campaigns were carried out (on 19th of June and 24th of September 2025). Measurements from these campaigns were complemented with an additional measurement campaign on the 8th of April 2026. These campaigns focused on physiological measurements on the 12 selected trees. Using a shotgun, branches of 30-50 cm length were shot from the south-facing side of the tree crown. Once harvested, the branches were submerged into water and recut to prevent rapid dehydration, after which the following steps and measurements were taken.

2.3.1 Gas exchange

Gas exchange measurements, including stomatal conductance and photosynthesis, were performed on site using a Li-COR 6800 (Li-COR Inc., Lincoln, NE, USA) gas exchange device.

The photosynthetic measurements were focused on ‘point measurements’ which measure in situ gas exchange under current conditions.

Needles of the recut branch were enclosed into the LiCOR’s cuvette gasket with the temperature inside the gasket set to match midday-temperatures (20°C, 17°C and 12°C for June 2025, September 2025 and April 2026 resp.), the VPD to 1.5 kPa and CO_2 of 400. Once the needles’ gas exchange performance had acclimated to the conditions in the cuvette (approx. 10 minutes), their photosynthetic activity was logged three times over one minute and then averaged. During the measurements on the 8th of April 2026, the LiCOR exhibited temperature sensitivity between 10:30 and 12:30, resulting in an offset which was noted and interpolated in order to be able to correct the A-value measurements in R.

The gas exchange measurements were thereafter corrected for the actual leaf area. For this, the needles inserted in the cuvette were marked, then, once measurements were complete, clipped off and gathered in a separate bag for overhead scanning in the lab.

The *projected leaf area* was measured by removing all needles from the twig part that was enclosed in the cuvette, photographing them on a flat surface and calculating leaf area with image J (Schneider et al. 2012). Projected leaf area was then multiplied with 3.2 to get to total leaf area (Goisser et al., 2016; Hesse et al., 2024).

2.3.2 Turgor loss point

In accordance with the protocol established by Bartlett et al. (2012), a 20cm long side-twig was cut from the main branch and put into double bags with a wet kitchen towel to limit transpiration and transported to Alnarp in a cooling box. At Alnarp's laboratories, the branches were recut under water, then left covered with an opaque plastic bag in a cool place to rehydrate over night, before measuring the osmotic potential of the needles.

Two to three needles were taken off the branch and aligned on a sheet of graph paper marked at 2mm x 6mm to cut a 12 mm^2 needle sample with a scalpel. This method was chosen over the more commonly used leaf disc created with a hole puncher, as it proved less useful for needles. The samples were transferred into the prepared aluminium envelope and submerged in liquid nitrogen for at least two minutes to destroy any cell structures in the needle. The needles were punctured with a pair or forceps and transferred to the osmometer chamber (Vapro 5600, Wescor). Total handling time stayed below 30 seconds. The osmometer was set to "Auto Repeat" mode and every of the 10 measurements noted in the protocol until two subsequent values differed no more than ± 5 mmol/kg.

Turgor loss point was then calculated by first converting the solute concentration c_0 (in mmol kg^{-1}) into osmotic potential at full hydration π_{osm} following formula a) below (van 't Hoff equation).

$$a)\ \pi_{osm} = (Rx\ T)/1000c_0$$

In a) R stands for the ideal gas content, T for temperature in degrees Kelvin. Then, the regression described by Bartlett et al. (2012) was used to estimate Leaf water potential at turgor loss point.

$$\pi_{tlp} = 0.832\ \pi_{oss}\ ^{-0.631}$$

2.3.3 Needle morphology

Needle morphology data was gathered from needles taken off the harvested side-branches.

Since the treatment roofs were finished in April 2025 and thus affected only the generation of needles developed in 2025, it was assumed in the model that the fixed factors year (2024 or 2025) and treatment, as well as site and treatment do not interact with each other in 2024, and the model adapted accordingly.

In the lab, the needles were analysed by year, with each nodule representing one individual year. Shoot length of 2025 and 2024 grown shoots was measured using a ruler. The needles were placed in paper envelopes and dried for 72h at

60°C. Dry weight was measured thereafter using a precision Scale (0.001 g resolution, OHAUS, Parsippany, NJ, USA).

From the total leaf area and dry weight measurements the *specific leaf area (SLA)* was calculated, which is a function of the projected leaf area divided by its dry mass.

2.3.4 Stem-water potential ψ_{stem}

A total of 12 trees (six roof, six control) is equipped with stem water potential sensors (FloraPulse microtensiometers, Davis, CA, USA) since April 2025, logging every 20 minutes.

The stem-water potential sensors (FloraPulse) detect changes in stem water potential, as stomatal conductance responds to changes in atmospheric transpiratory demand (vapor pressure deficit, VPD) and soil water (Kahdke et al., 2026). It is assumed, that once stomata close to prevent further transpiration, leaf and stem water potential equilibrate (Rodriguez-Dominguez et al., 2025). Stem water potential is described by Rodriguez-Dominguez et al. (2025) as an important variable to contextualise the linkages drought responses to specific plant traits.

Due to continuous malfunction, one of the 12 sensors had to be excluded from the dataset.

2.4 Statistical analysis

The collected data was statistically analysed in R (4.5.1.) using R Studio (2025.09.0+387), to assess whether the two explanatory factors, namely the xeric or mesic growing conditions and the treatment (drought/ ambient) can explain differences in the response variables , turgor loss point (π_{tlp}) , gas exchange (*A,* g_{sw}, and *iWUE),* ψ_{stem} and needle morphology.

All parameters were analysed using two-way ANOVA with site (xeric / mesic) and treatment (roof) as fixed factors. For measurements that were repeated in 2025 and 2026 (morphology, gas exchange, ψ_{stem}) separate models for each measurement date were employed, both for the sake of model convergence and to simplify the three-way interactions that appeared in the larger model with date included.

F- and p-values were derived using ANOVA available via the ‘car’ package, using Satterthwaite’s method. We tested for the normality of residuals using Q-Q-plot; however, no outlier transformation was needed.

A post-hoc tests for the linear regression model was performed using the TukeyHSD test (Faria et al. 2015), whenever a interaction tested statistically significant .

3. Results

3.1 Precipitation & Volumetric soil water content

Influence of precipitation on volumetric soil water content

Precipitation varied during 2025, averaging at 1.28mm per day and a sum total of 470.1mm, with peaks in mid-July, early August and late September (Figure 2). In spring 2026 precipitation levels were comparable to those of the previous year.

After the sensors were installed in April 2025, VWC decreased from an average 0.38 $m^3 m^{-3}$ around control trees and average 0.28 $m^3 m^{-3}$ around treatment trees to an average of 0.24 $m^3 m^{-3}$ for control and 0.13 $m^3 m^{-3}$ by June 2025. Thereafter it increased for a few days, due to rainfall and declines again until heavier precipitation in September. The VWC measurements then stabilise during the winter months to around 0.33 $m^3 m^{-3}$ for control and 0.17 $m^3 m^{-3}$ for treatment in mid-March.

Treatment effects on soil water content

The sharp peaks of the VWC measurements near the control trees on both upper and lower site indicates that precipitation increases volumetric soil water content for a few days (Figure 4), mostly due to the placement of the sensors in the topsoil. This dynamic is in line with a low water holding capacity of the soil.

The measurements for the roofed tree group indicate a relative stable effect of the throughfall exclusion roofs on VWC, when compared to the control group.

On average, treatment trees experience 0.1 $m^3 m^{-3}$ lower VWC than the control during the summer months. The precipitation during the winter and early spring registered in patches, possibly due to the low temperatures at the site during this time. However, the soil water content data indicates a recovery of VWC over the course of winter and spring, especially after snow melt at the end of February.

Even the measurements near the roofed trees register a slight upturn of volumetric soil water content during the winter months, indicating a light recovery.

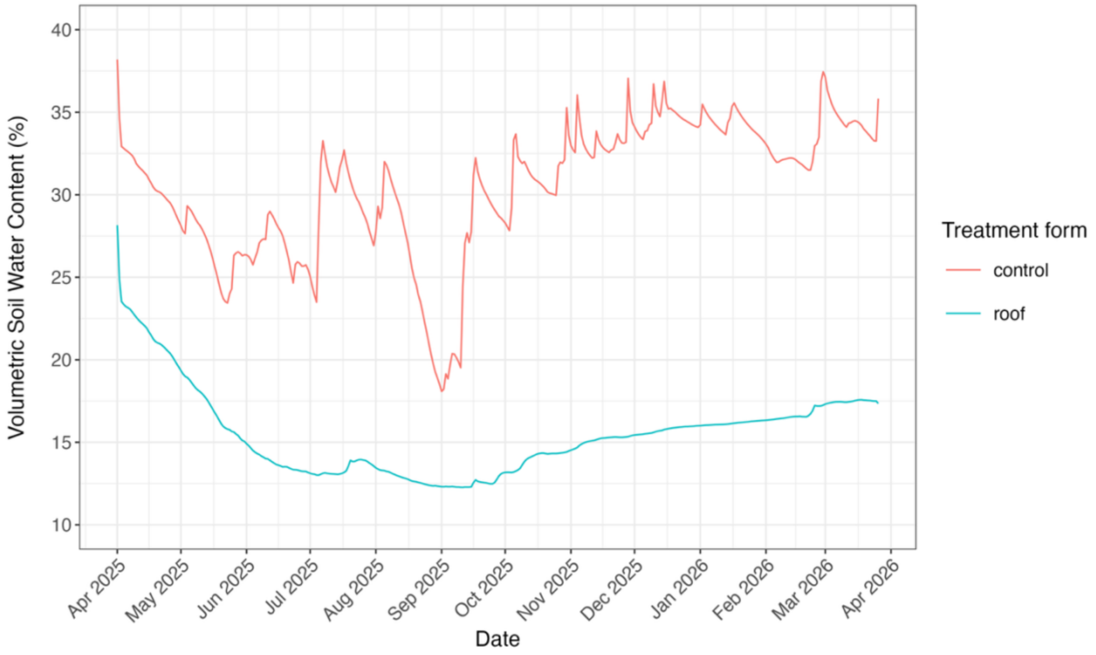

Figure 4 *Volumetric Soil Water Content by treatment measured at the experimental site from April 2025 to April 2026. Volumetric Soil Water Content data provided by Dr. Maartje Klapwijk, Department of Ecology, SLU Uppsala.*

3.2 Stem water potential ψ_{stem}

While site had no significant effect on ψ_{stem} , roofs significantly caused reductions in ψ_{stem} in June ($p < 0.001$), even though most trees maintained a ψ_{stem} of -0.75 MPa or higher over the experimental period (see Figure 5; Table 2). Mild drought stress is generally reached at -1.0 to -1.5 MPa, however recent work in adult Norway Spruce by Arend et al. (2021) showed, that Norway spruce reaches its point of stomatal closure (P_{ST}) at -2.1MPa and its tipping point for increased mortality at -2.4 MPa, leaving a non-linear hydraulic safety margin of 0.3 MPa until it reaches mortality (P50) at -3.5 MPa.

The severity of the drought stress was alleviated in September, and trees could recover even more over the winter months. No statistically significant effect of neither treatment nor site could be found in September or April. Table 2 below provides an overview of the statistical analysis of ψ_{stem}.

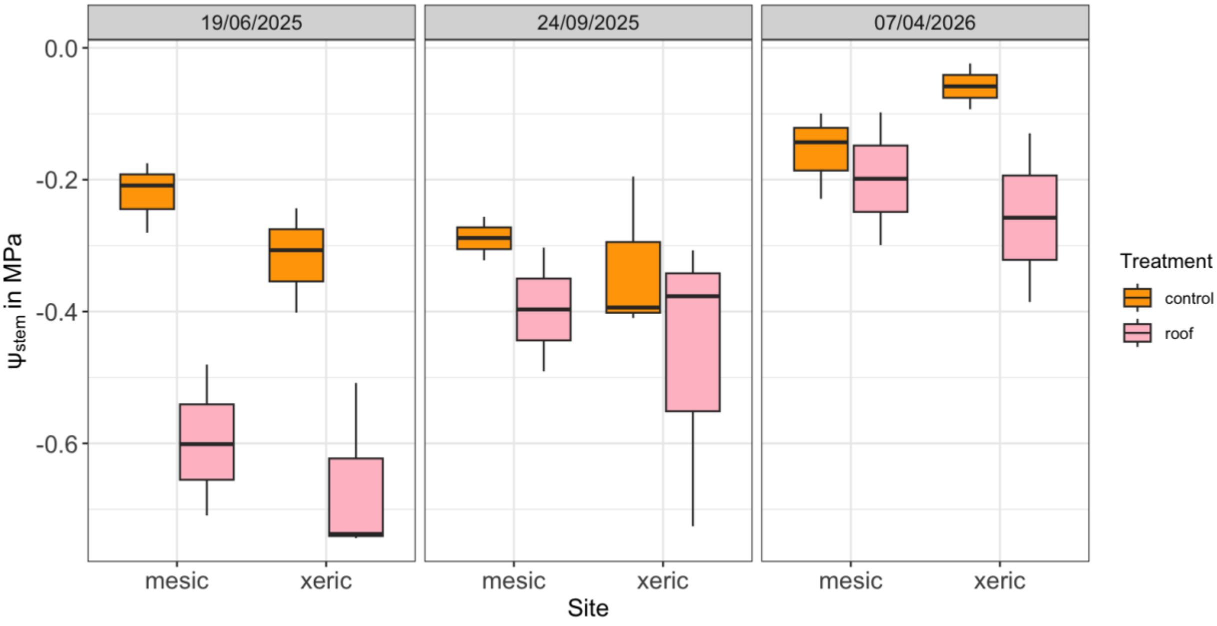

Figure 5 *ψ_{stem} in MPa of all trees per site category and treatment (pink). Each box represents the variation, relative to the median (black line) with error bars for outliers. Due to power loss in mid-August, only partial measurements were taken on September 24th. Tree 71 had to be removed, due to the attached sensor malfunctioning. Data provided by Dr. Schönbeck, Southern Swedish Forest Research Centre.*

Table 2 *Overview table of the statistical analysis of variance(type II) for minimum ψ_{stem} measurements. Baseline for the factors were site = mesic and treatment =control. Statistically significant values are highlighted bold.*

	Estimate	Std. error	F-statistic	p-value
$\boldsymbol{\psi}_{\textbf{stem}}$				
June				
Site (mesic – xeric)	-0.958	0.820	1.953	0.199
Treatment (control – roof)	-3.755	0.820	38.699	**0.0002**
Site* Treatment	0.296	1.159	0.065	0.804

	Estimate	Std. error	F-value	p-value
September				
Site (mesic – xeric)	-0.440	1.191	0.615	0.458
Treatment (control – roof)	-1.078	1.331	1.951	0.205
Site* Treatment	-0.290	1.786	0.0264	0.875
April				
Site (mesic – xeric)	0.988	1.033	0.043	0.843
Treatment (control – roof)	-0.413	1.033	2.195	0.198
Site* Treatment	-1.578	1.532	1.061	0.350

3.3 Gas exchange

In the results, the focus will be on the summer measurements, as June showed the strongest differences in site and treatment effect when compared to later measurements (Figure 6).

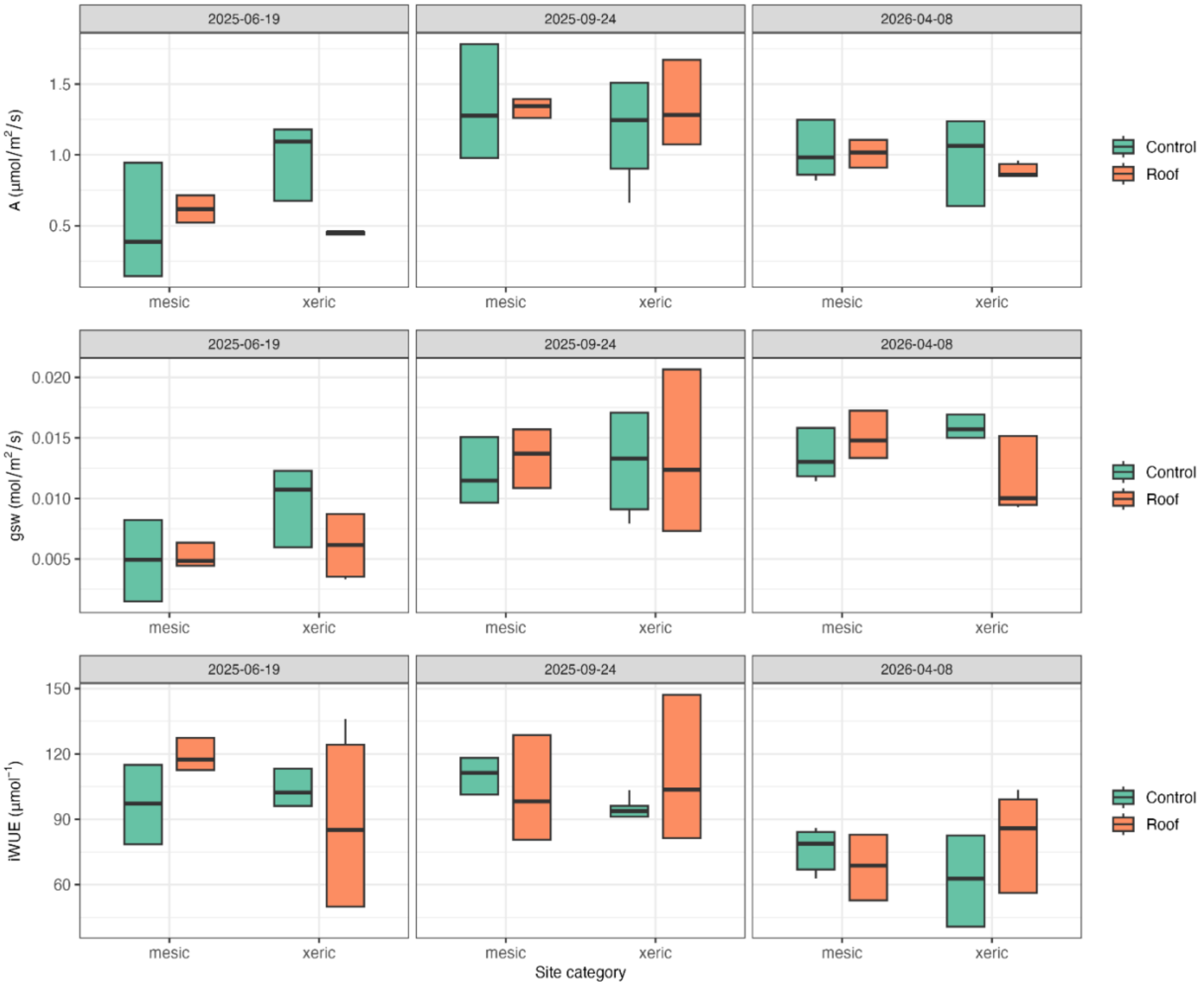

Figure 6 *Photosynthetic activity (A in µmol/m^2/s), gas exchange (g_{sw} in mol/m^2/s) and intrinsic water use efficiency (iWUE in µmol^{-1}) grouped by measurement date, microsite category and treatment. Each box represents the variation, relative to the median (black line) with error bars for outliers.*

Photosynthetic activity (A)

In June, when signs of drought were most expected, a long-term acclimation was observable in the photosynthetic activity of xeric control trees, but the sudden drought caused by roofs impacted these xeric trees more than mesic trees (interaction roof x site: $p < 0.001$; Table 4).

Roofs significantly reduced photosynthesis on xeric sites (0.43 ± 0.007 µmol/m^{-2}/s^{-1}) compared to the controls (0.55 µmol/m^{-2}/s^{-1} difference; $p < 0.001$) and further caused reductions in photosynthesis on mesic sites by 0.12 µmol/m^{-2}/s^{-1}, supporting a treatment effect (Table 3).

High levels of photosynthesis were observed in the control trees on the xeric site (0.98± 0.07 µmol/m^{-2}/s^{-1}), while on the mesic site control trees showed significantly lower photosynthetic activity (0.49± 0.11 µmol/m^{-2}/s^{-1}; $p < 0.001$) in comparison, revealing a long-term site acclimation effect.

During September of 2025 the analysis showed no statistically significant effect of neither treatment nor site on photosynthesis (all $p > 0.05$). Results from measurements taken on April 8th, 2026, show no statistically significant effect of any explanatory variables on the photosynthetic rate either ($p > 0.05$ for all combinations).

Table 3 Overview of mean gas exchange variables for photosynthetic activity A, stomatal conductance g_{sw} and intrinsic Water Use Efficiency iWUE.

Variable (unit)	Xeric + roof	Xeric + control	Mesic + roof	Mesic + control	Month
A (µmol/m^{-2}/s^{-1})	0.43 ± 0.04	0.98 ± 0.07	0.61 ± 0.02	0.49 ± 0.11	June
	1.34 ±0.08	1.16 ± 0.11	1.33 ± 0.02	1.34 ± 0.11	September
	0.88 ± 0.01	0.98 ± 0.08	1.01 ± 0.02	1.03 ± 0.06	April
g_{sw} (mol/m-^{2}/s^{-1})	0.0060 ± 0.0009	0.0096 ± 0.0009	0.0052 ± 0.0002	0.0048 ±0.0009	June
	0.013 ± 0.001	0.012 ± 0.001	0.013 ± 0.0007	0.012 ± 0.0007	September
	0.011 ± 0.0009	0.015 ± 0.0002	0.015 ± 0.0005	0.013 ± 0.0006	April
iWUE (µmol/mol^{-1})	89.05 ± 13.05	103.88 ± 2.90	119.15 ±2.40	96.89 ± 5.80	June
	110.70 ± 9.82	93.65 ± 4.42	102.51 ± 7.24	110.29 ±2.46	September
	79.31 ± 6.69	62.00 ± 6.08	68.16 ± 4.41	76.22 ± 3.14	April

Stomatal conductance (g_{sw})

A similar long-term site acclimation effect to the one observed in A could be found in the stomatal conductance, while the treatment does not show the same impact pattern in g_{sw}.

Roofs on xeric sites caused lower mean stomatal conductance (0.0060 mol/m- ^{2}/s^{-1} ± 0.0009) compared to control trees, which showed the highest mean stomatal conductance (0.0096± 0.0009 mol/m^{-2}/s^{-1}; $p = 0.01$) across site and treatment groups during June, while the control group on the mesic showed the lowest (0.0048 ±0.0009 mol/m^{-2}/s^{-1}). During this month, both treatment and site, as well as their interaction had a significant effect on stomatal conductance (all $p < 0.03$). Xeric and mesic control groups differed by 0.0048 mol/m-^{2}/s^{-1} ($p < 0.001$), supporting a long-term site effect (Table 4).

During September, mean stomatal conductance across both sites and treatments increases compared to June and shows little variation between treatments (Table 3). In September 2025 treatment had little effect on g_{sw}, but the reverse was noticeable in April, when roofs caused a reduction of g_{sw} on the xeric site (0.011 ± 0.0009 mol/m-^{2}/s^{-1}) compared the mesic site (0.015 ± 0.0005 mol/m-^{2}/s^{-1}). The post hoc test showed this difference to be significant ($p = 0.006$). Together, these outcomes indicate seasonal differences in stomatal conductance, which are exacerbated by the treatment.

Intrinsic Water Use Efficiency (iWUE)

Results for iWUE show none of the previous long-term acclimation pattern, nor of cohesive short-term drought impacts across groups.

Nevertheless, during June, the lower iWUE of roofed trees on the xeric site showed a barely significant ($p = 0.04$) tendency compared to roofed trees on the mesic sites. Interestingly, in the same month, the mesic control showed lower iWUE than the roofed trees on the same site (Table 3), hinting at a treatment effect mainly on the xeric site. This is supported by the analysis which revealed a significant interaction of treatment and site all measurement dates ($p \leq 0.03$).

The aforementioned dynamic was reversed in September, when roofed trees showed higher iWUE on the xeric site than on the mesic, while the xeric control exhibited the lowest overall mean iWUE measurements (93.65 ± 4.42 μmol/mol^{-1}). In April 2026, roofed trees on the xeric site again showed higher iWUE compared to those on the mesic site and the xeric control the lowest (62.00 ± 6.08 μmol/mol^{-1}), although not significantly lower than the mesic control group.

Table 4 *Estimate, standard error and statistics of the Anova for A, g_{sw}, iWUE on the measurement days. Baseline for the factors were site = mesic and treatment =control. Statistically significant values are highlighted bold.*

	Estimate	Std error	F-statistic	p-value
A				
June				
Site (mesic – xeric)	0.491	0.069	3.116	0.08
Treatment (control – roof)	0.126	0.097	11.941	**0.001**
Site* Treatment	-0.669	0.134	24.971	**1.619 e^{-05}**
September				
Site (mesic – xeric)	-0.180	0.131	1.045	0.313
Treatment (control – roof)	-0.012	0.140	0.847	0.363
Site* Treatment	0.188	0.193	0.957	0.334
April				
Site (mesic – xeric)	-0.059	0.077	2.966	0.094
Treatment (control – roof)	-0.028	0.077	1.215	0.278
Site* Treatment	-0.064	0.110	0.344	0.561
G_{sw}				
June				
Site (mesic – xeric)	0.004	0.001	10.131	**0.003**
Treatment (control – roof)	0.0003	0.001	4.675	**0.037**
Site* Treatment	-0.003	0.001	5.743	**0.022**
September				
Site (mesic – xeric)	0.0008	0.001	0.090	0.765
Treatment (control – roof)	0.001	0.001	0.505	0.481
Site* Treatment	-0.0008	0.002	0.098	0.755
April				
Site (mesic – xeric)	0.002	0.0009	0.832	0.367
Treatment (control – roof)	0.001	0.0009	3.873	0.057
Site* Treatment	-0.005	0.001	17.650	**0.0001**
iWUE				
June (mesic – xeric)				
Site	6.990	11.687	2.507	0.122
Treatment (control – roof)	22.257	11.687	0.096	0.757
Site* Treatment	-37.083	16.003	5.369	**0.026**

September				
Site (mesic – xeric)	-16.639	7.913	0.891	0.351
Treatment (control – roof)	-7.786	8.459	0.892	0.351
Site* Treatment	24.832	11.583	4.596	**0.039**
April				
Site (mesic – xeric)	-14.219	7.414	0.061	0.806
Treatment (control – roof)	-8.061	7.414	0.777	0.384
Site* Treatment	25.364	10.484	5.852	**0.021**

3.4 Turgor loss point

One year after the start of the treatment, no significant differences in turgor loss point were found (Figure 7). On xeric sites, roofs tended to cause a reduction in mean turgor loss point (-1.52 MPa), indicating a response to the drought treatment that leads to higher drought tolerance, although the effect was insignificant ($p > 0.05$; Table 5). In contrast, on mesic sites, roofs resulted in a higher turgor loss point compared to control (-1.36 MPa). The mean π_{tlp} for the control trees differed less from each other, with -1.40 MPa for the xeric site and -1.47 MPa for the mesic sites, thus showing a tendency of a long-term site effect that is enforced by the treatment.

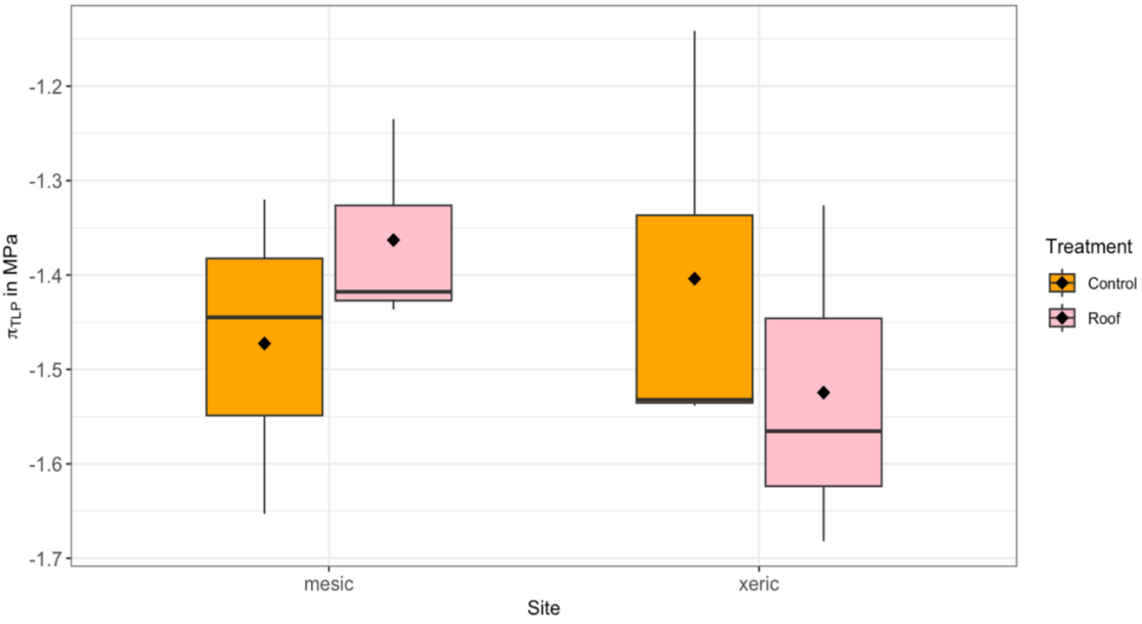

Figure 7 *Turgor loss point (MPa) of sampled sun-needles from April 2026 by treatment and site category. Each box represents the variation, relative to the median (black line) and the mean (black rhombus) with error bars for outliers.*

Table 5 *Overview table of the statistical analysis of variance (Type II) for π_{tlp} measurements. Baseline for the factors were site = mesic and treatment =control. Statistically significant values are highlighted bold.*

	Estimate	Std. error	F-statistic	p-value
π_{tlp}				
Site (mesic – xeric)	0.023	0.051	0.206	0.661
Treatment (control – roof)	0.002	0.051	0.0029	0.958
Site* Treatment	-0.057	0.051	1.267	0.292

3.5 Needle morphology

There are no signs of long-term morphological acclimation between the two site categories. The one-year roof treatment did not cause significant differences between control and roof trees (p>0.05 for site and treatment as explanatory variables) (Table 7). Similarly, the site elevation or treatment had no significant effect on the variation on either SLA or needle length, and none of the possible explanatory variables affected the shoot length significantly (Figure 8). Thus, there is little evidence for a long-term site acclimation of the needles.

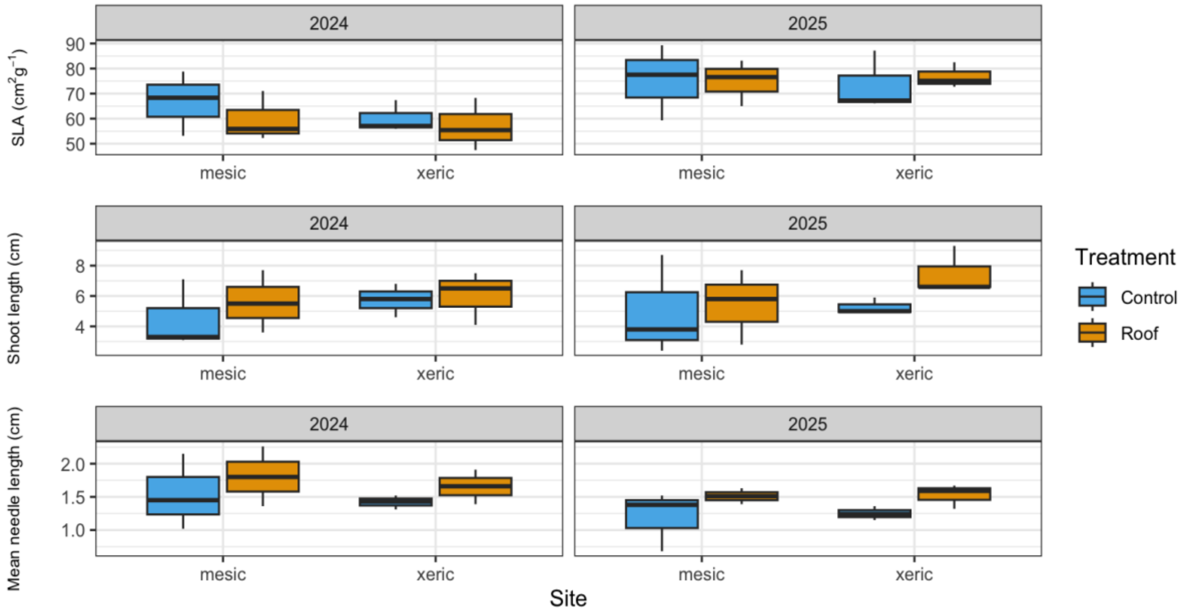

Figure 8 *Overview (top to bottom) of the Specific Leaf Area (cm^2g^{-1}), shoot length (cm) and needle length (cm) by treatment, site category and generation. Each box represents the variation, relative to the median (black line) with error bars for outliers.*

Interestingly though, roof trees in xeric sites showed the largest increase in shoot length between 2024 and 2025, compared to the other groups. Table 6 below depicts the average of each variable per generation, microsite and treatment combination (Table 7; Figure 8). Furthermore, an interesting size reversal can be observed in the SLA of the roofed trees on the xeric site, which increased from least area to the largest in 2025. The same trees also increased their shoot length but lost on average 14mm in needle length between 2024 and 2025 (Table 6).

Table 6 Average SLA, shoot length and needle length values per year, site category and treatment form. N=3 for every subgroup and variable.

Variable	Year	Mean + SE	Model
SLA (cm^2 g^{-1})	2024	57.0 cm^2 g^{-1} ± 6.06	Roof + xeric
		59.7 cm^2 g^{-1} ± 5.74	Roof + mesic
		60.1 cm^{2}g^{-1} ± 3.64	Control+ xeric
		66.8 cm^{2}g^{-1} ± 7.44	Control + mesic
SLA (cm^2 g^{-1})	2025	75.1 cm^{2}g^{-1} ± 2.94	Roof + xeric
		76.6 cm^{2}g^{-1} ±5.30	Roof + mesic
		67.2 cm^{2}g^{-1} ±6.84	Control+ xeric
		77.5 cm^{2}g^{-1} ±8.71	Control + mesic
Shoot length	2024	6.03 cm ±1.00	Roof + xeric
		5.60 cm ±1.18	Roof + mesic
		5.73 cm ± 0.63	Control+ xeric
		4.50 cm ± 1.30	Control + mesic
Shoot length	2025	7.50 cm ±0.90	Roof + xeric
		5.43 cm ±1.42	Roof + mesic
		5.25 cm ±0.31	Control+ xeric
		4.96 cm ±1.90	Control + mesic
Needle length	2024	1.65 cm ± 0.15	Roof + xeric
		1.80 cm ±0.25	Roof + mesic
		1.42 cm ± 0.06	Control+ xeric
		1.54 cm ± 0.32	Control + mesic
	2025	1.52 cm ± 0.10	Roof + xeric

Needle length	1.51 cm ± 0.06	Roof + mesic
	1.25 cm ± 0.06	Control+ xeric
	1.19 cm ± 0.25	Control + mesic

Table 7 Overview table of the statistical analysis of variance(type II) for needle morphology measurements. Baseline for the factors were site = mesic and treatment =control. Statistically significant values are highlighted bold.

	Estimate	Std. error	F-statistic	p-value
SLA				
2024				
Site (mesic – xeric)	-6.633	8.322	0.628	0.450
Treatment (control – roof)	-7.023	8.322	0.737	0.415
Site* Treatment	3.937	11.769	0.111	0.746
2025				
Site (mesic – xeric)	-1.873	8.933	0.000	0.999
Treatment (control – roof)	-0.460	8.933	0.496	0.829
Site* Treatment	3.733	12.633	0.087	0.775
Shoot length				
2024				
Site (mesic – xeric)	1.233	1.503	0.614	0.455
Treatment (control – roof)	1.100	1.503	0.433	0.528
Site* Treatment	-0.800	2.126	0.141	0.716
2025				
Site (mesic – xeric)	0.300	1.815	0.848	0.383
Treatment (control – roof)	0.466	1.815	1.105	0.323
Site* Treatment	1.766	2.567	0.473	0.510

	Estimate	Std. error	F-statistic	p-value
Needle length				
2024				
Site (mesic – xeric)	1.233	1.503	0.614	0.455
Treatment (control – roof)	1.100	1.503	0.433	0.528
Site* Treatment	-0.800	2.126	0.141	0.716
2025				
Site (mesic – xeric)	0.056	0.208	0.061	0.810
Treatment (control – roof)	0.316	0.208	4.036	0.079
Site* Treatment	-0.04	0.295	0.018	0.895

4. Discussion

The aim of this thesis was to reveal the impact of long-term acclimation to site elevation on the physiological and morphological drought response of Norway spruce. No evidence of a morphological drought acclimation response could be found in the needles and shoots of the roofed and control trees on either microsite. Similarly, no physiological acclimation of the turgor loss point as a reaction to the drought simulation could be measured after one year.

However, the gas exchange measurements showed a significant difference between xeric and mesic sites, insofar as the photosynthesis of treatment trees on the xeric site was more negatively affected during June, while the control trees on the xeric sites could maintain high mean levels of photosynthesis and stomatal conductance. This indicates that xeric acclimated trees could uphold photosynthetic activity during the drier summer months, but the treatment caused them to reduce photosynthesis as a reaction to the sudden drought. In the same month, the strongest reductions of g_{sw} were observed in the control trees on the mesic site, which lends further support to the conclusion, that a long-term site acclimation of stomatal sensitivity is present, but subject to seasonal variations, which are further enforced by the treatment.

4.1 Rejecting or accepting the working hypothesis

At the beginning of this thesis (see section 1.1.1), the following working hypotheses were stated:

H_1: *Trees acclimated to long-term xeric conditions have reduced sensitivity of stomates to sudden drought, resulting in higher levels of photosynthetic activity under drought compared to trees acclimated to mesic conditions.*
In summer, when drought effects were most expected, xeric treatment trees exhibited lower gas exchange, especially photosynthetic activity, compared to mesic treatment trees. While the higher gas exchange of control trees on the xeric site compared to the control trees on the mesic site did support the presence of long-term site acclimation, we could not find sufficient evidence of reduced sensitivity to sudden drought. Therefore, H_1 has to be rejected.

H_2: *Physiological acclimation (e.g. needle turgor loss point, stomatal closure) in Norway spruce occurs both in response to long-term and short-term soil moisture changes. Turgor loss point is expected to be lower in xeric conditions and in response to short-term drought.*
Needle turgor loss points (π_{tlp}) of roofed trees on the xeric site was the most negative, followed by the control group on either site category, and the least negative π_{tlp} was found in the roofed trees on the mesic site. This indicates that a long-term physiological acclimation has indeed occurred, but the findings do not support a significant response in π_{tlp} to short-term soil moisture changes. Therefore, H_2 has to be rejected in regard to a response of short-term physiological acclimation.

H_3: *Long-term acclimation to soil moisture results in smaller needles with a lower specific leaf area, while one growing season of drought did not yet affect needle morphology.*

Based on the results, **H_3** can be fully rejected, since needles were not found to be significantly different between treatments for each of the variables – SLA, shoot length, leaf area. Furthermore, site conditions had no discernible effect on any of the needle morphology variables, giving thus no support to a long-term acclimation to soil moisture availability.

4.2 Short- and long-term acclimation of physiological traits

Across the measured physiological and morphological variables, the xeric control trees generally showed signs of higher drought resilience, than the mesic control. For example, median π_{tlp} and g_{sw} of xeric control trees were higher during June, when drought effects were most expected, thus supporting the conclusion that long term physiological acclimation to site was indeed present.

4.2.1 Higher sensitivity to sudden drought in trees acclimated to xeric conditions

Contrary to our expectations in H_1, trees acclimated to xeric conditions responded to the drought treatment with a stronger reduction of assimilation (*A*) than on mesic conditions. These observations are in line with the findings of Ge et al. (2011), who described a comparatively early and rapid decline of canopy conductance in Norway Spruce on dry sites.

One possible explanation is that the roofs may have caused more severe drought stress on xeric sites than prior drought events in one of Sweden's more precipitation rich areas (SMHI n.D.). Arend et al. (2021) were able to show that hydraulic decline in mature Norway Spruce happens both non-linear and much earlier than previous studies on potted seedlings had found. While minimum ψ_{stem} observations show that xeric treatment trees approached mild drought stress only during June, specifically June precipitation was shown to have a significant effect on Norway Spruce growth, by Ogana et al.(2024). Furthermore, the VWC measurements near xeric treatment trees confirm a steady decline of available soil water during this period (Figure 4).

Similarly, Levesque et al. (2013) found the radial growth of Norway Spruce on mesic sites to be less impacted by drought in the previous year than Norway Spruce on xeric sites. This indicates a slower reduction in the gas exchange of trees accustomed to relatively higher soil water availability, which aligns with our findings for June.

In the same month, we further observed the strongest reductions of g_{sw} in the control trees on the mesic site, together with a strong though non-significant tendency of higher g_{sw} in treatment trees on the xeric site compared to treatment trees on the mesic site. More long-term data is necessary to determine whether this is a consistent trend and the start of acclimation to new growing conditions. For example, Hesse et al. (2024) describe in their study, how mature Norway spruce in a similar throughfall experiment in Bavaria were able to reduce its total water use by closing its stomata by up to 80% in the first two summers of their trial setup. The authors describe stomatal closure as a first drought mitigation step preceding a reduction of canopy from the second summer onwards, in their five years spanning study.

Another possibility for drought mitigation is the passive relocation of water, so called hydraulic relocation (HR). Authors such as Hafner et al. (2017) found Spruce to be able to redistribute available soil moisture to drier areas via its roots, to maintain their cell-structure under drought. This water transfer also shifts co-located nutrients and can affect other species with roots in the drier areas. HR coupled with the heterogeneous elevation structure of the site could make it possible, that trees benefited from the hydraulic redistribution of their neighbouring trees with partial roots outside the roofs (Hafner et al., 2021; 2026).

This could have allowed target trees to maintain stomatal openings during June, however, since Hafner et al. (2020; 2026) conducted their studies on seedlings as recipients, the results' transferability to a mature stand have to be viewed with caution.

4.2.2 Physiological acclimation to sudden drought

We found trees acclimated to xeric growing conditions to have a more negative π_{tlp} than those in mesic growing conditions. A more negative turgor loss point is considered indicative of higher drought tolerance (Guzzon et al., 2026), and likely allowed those trees to maintain stomatal conductance, photosynthesis and growth under lower water availability, as previously found by (Zhu et al., 2018).

A comparative study into leaf turgor loss point as a predictor of drought resistance for Norway Spruce and 15 other common tree species across Central Europe by Kunert et al. (2024) confirmed its usefulness as a direct metric for plant drought tolerance over larger spatial scales. However, Kunert et al. (2024) measured π_{tlp} during intense drought events (2018 – 2020) in Central Europe in relation to growth anomalies derived from basal area and do not report any shifts of πtip in comparison to a pre-drought baseline.

Even though we found differences in π_{tlp} as induced by long-term acclimation, we did not find any acclimation in response to the roof treatment. It is possible that the observed reduction of g_{sw} were sufficient to mitigate the drought effects in the first year, since temperatures, which are mentioned by Kunert et al. (2024) as another important factor in decreased gas exchange in response to drought, were lower in June 2025 than in July or August the same year. A drought release study conducted by Hesse et al. (2023) describes a slow recovery of π_{tip} over the course of one year to levels comparable to the control group. However, since the study was conducted during the intense drought years of 2019 and 2020 it is likely that the drought effect of the treatment in our thesis was either not severe enough or in effect too briefly to shift π_{tlp} significantly.

4.2.3 Morphological acclimation

The assessment of needle morphology in this thesis provided no statistically significant effect of treatment or microsite. Instead, needle length, shoot length and SLA of xeric treatment trees generally increased between 2024 and 2025.

Specific leaf area (SLA) is considered an indicator of the resource availability in a plant’s environment, with lower SLA indicating lower resource availability (Busch et al., 2024), however, we found no reduction in SLA in this experiment. These findings further stand in contrast to those by Gebauer et al. (2018), who showed that mild drought conditions were sufficient to influence the needle morphology of especially sun-needles, in terms of needle length, thickness, density, projected needle area and total needle area. Similarly, Hesse et al. (2024) observed, that drought stressed Norway Spruce adapted their shoot length during bud burst in spring, but further report shorter needles and shoots from the second summer since drought onset onwards (see also Zhu et al., 2022).

Furthermore, bud development in Norway spruce is induced by both day length and temperatures during fall of the previous year (Grossnickle 2000) and bud burst is initiated by spring temperatures (Svystun et al., 2021). Thus the ‘latest’ fully developed needles were induced prior to the drought onset and budburst in early March 2025 when mean temperatures increased past 5°C (Figure 2). It is most likely, that the shoots and needles measured in this thesis still would be little affected by the roofs, which were erected in early spring 2025.

Morphological acclimation and the drought-legacy effect

Morphological acclimation occurs on time scales from weeks to months or years, and thus slower and with a delay compared to physiological acclimation.

Functional traits, such as needle area, are essential for photosynthetic activity and its reduction a resource and time intensive adaptive step to reverse, as it will in turn affect the physiological process that power these reversing morphological changes (Zweifel et al., 2020). In a long-term study on needle morphology in Norway Spruce in Switzerland Zhu et al. (2022) reported that drought influences needle length and further found that a decline in needle mass per length was the main long-term adaptation to water stress, first noticed after two years of drought.

Hikino et al. (2025) highlight that both morphological and physiological drought acclimation responses occur non-linear, as they affect each other, as well as the morphological (e.g. canopy size increase) and physiological (e.g. π_{tlp}) recovery, the aforementioned drought legacy effect. This effect, however, has positive implications for drought resilience as well, as Norway Spruce with a drought legacy showed higher resilience towards the severe drought of 2022 in the middle of Hikino et al. (2025) recovery experiment.

4.2.4 Seasonal variations

The gas exchange measurements showed clear variations over the seasons, with the highest photosynthesis observed in xeric treatment trees during September 2025. The measurement campaign happened after a rain event in mid-September, which relieved the trees temporarily from drought. Literature has shown how trees can rapidly change their carbon uptake and allocation patterns in response to rewatering events (see e.g. Hagedorn et al., 2016; Joseph et al., 2020; Hesse et al., 2023), which we could observe in both xeric treatment trees and mesic control trees, who showed the strongest differences in assimilation (A) between June and September. The research on source-sink control dynamics in drought recovery by Hagedorn et al. (2016) further suggests, that drought causes a rapid compensation mechanism in the carbon flux to recompense for the missed intake and strengthen roots and mycorrhiza before the next drought.

In their drought recovery study, Hesse et al. (2023) also observed recovery of g_{sw} in drought stressed trees within three days after watering. G_{sw} data measured in this thesis during September aligns with the findings, however, g_{sw} levels of roofed trees on the mesic microsites were lower than both the roofed xeric site and their mesic control during September and April. Interestingly, while g_{sw} in xeric control and mesic treatment trees remained high in April, photosynthesis decreased across groups. Simultaneously, VWC on both sites increased lightly during the winter months (Figure 4), while the available minimum ψ_{stem} data indicates, that the treatment trees experience at most very mild drought stress in spring 2026, despite the decrease in photosynthesis measured in April and the overall lower g_{sw} of treatment trees on mesic sites.

4.3 Limits in scope of the thesis

The drought response in Norway Spruce is influenced by a multitude of factors such as the relative temperature increase (see e.g. Dusenge et al., 2020; Goude et al., 2022), precipitation patterns prior to drought onset as well as during the drought (Ogana et al., 2024), prior drought events (Lévesque et al. 2013), time in growing cycle (Zhu et al., 2022), elevation and topography (Gutierrez Lopez et al. 2021), stand density and composition (Pardos et al., 2021), nutrient status and height (Niinemets, 2002), which all interact with each other. Attempting to accurately capture these interactions would far exceed the scope of a master thesis, especially within one year.

Data was limited by the relatively small sample size (12) and runoff may affect the drought severity each tree was experiencing differently, due to the irregular terrain of the site and the unknown size of each tree's root system. The data analysed in this thesis was further gathered in a newly established experiment (<1 year since establishment), which limits its temporal distribution of the gathered data to one year.

To account for the time constraints, soil water and stem water potential measurements were taken on a high time resolution. Additionally, photosynthesis was measured multiple times in 2025 and 2026, to get a more robust dataset. It was nevertheless not possible to determine, whether the roofed trees on the mesic site increased their drought resilience after the first season of drought. Data from coming years is necessary to show any significant change.

Lastly, the experimental design differs from previous roofed drought experiments in Sweden, (see e.g. Nilsson (1993)), due to its non-seasonal drought simulation. It thus presents an opportunity to study the initial phase of a prolonged drought in detail, which can inform carbon sequestration estimates and further research into raising the resilience of stands to seasonal drought.

5. Conclusion

Utilizing a roof experiment that exposes trees in xeric and mesic microsites to drought by decreasing the amount of precipitation throughfall, this thesis set out to investigate the impact of long-term acclimation to site elevation induced soil-moisture on the physiological and morphological drought response of Norway spruce.

The outcomes show that morphological acclimation is not observable as a reaction to a year of drought exposure. However, physiological acclimation in form of turgor loss point adjustments were measured and part of the long-term physiological acclimation strategy of the trees. Furthermore, the gas exchange measurements support, that the trees acclimated to the xeric microsites can uphold photosynthetic activity to a comparable level to trees acclimated to mesic microsites during summer but reduced it significantly in reaction to the treatment.

The measurements of g_{sw} specifically also lend support to the conclusion roofed trees on the xeric site recover quickly, in terms of both short-term gas exchange increases after precipitation and with increasing volumetric soil water content during the winter months. This is tentatively supported by ψ_{stem} measurements, which show that treatment trees experienced a seasonal recovery from September to April. Whether morphological adaptation processes to decrease evaporative demand have started will become clearly visible with spring flush in 2027.

The central learning of these results is therefore, that Norway Spruce can resist mild to moderate drought stress with mainly physiological responses, namely seasonal reductions of photosynthesis, without physiological acclimation. More and more long-term data is needed to enhance our understanding of short- and long-term acclimation of these trees and develop concrete measures for increasing drought resilience in Norway Spruce stands.

Possible new avenues present themselves in research on mixed stands of spruce and Scots Pine (*Pinus sylvestris*) or spruce, pine and birch mixtures to mitigate drought impacts (see e.g. Pardos et al., 2021). The authors identified greater resilience in broadleaf – conifer-mixtures than in a two conifer species mixture, which in turn showed higher resilience than conifer monocultures. Investigating the ecophysiological processes behind these observations could provide valuable insights into e.g. the resilience failure thresholds toward drought intensity or temperature increases these species-mixtures can withstand and thereby inform silvicultural practice for climate chance mitigation and adaptation.

References

Aldea, J., Dahlgren, J., Holmström, E. & Löf, M. (2023). Current and future drought vulnerability for three dominant boreal tree species. *Global Change Biology*. 30 (17079). Wiley. https://doi.org/DOI:%2010.1111/gcb.17079

Anon (2026). Reference climate data from the Unit for Field-based Forest Research climate monitoring program. https://www.slu.se/esf-referenceclimate/ [2026-02-25]

Arend, M., Link, R.M., Patthey, R., Hoch, G., Schuldt, B. & Kahmen, A. (2021). Rapid hydraulic collapse as cause of drought-induced mortality in conifers. *Proceedings of the National Academy of Sciences*, 118 (16), e2025251118. https://doi.org/10.1073/pnas.2025251118

Bartlett, M., Scoffoni, C., Ardy, R., Ya, Z., Shanwen, S., Cao, K.-F. & Sack, L. (2012). Rapid determination of comparative drought tolerance traits: Using an osmometer to predict turgor loss point. *Methods in Ecology and Evolution*, 3, 880–888. https://doi.org/10.1111/j.2041-210X.2012.00230.x

Bundesministerium für Ernährung und Landwirtschaft (2022). Der Wald in Deutschland - Ausgewählte Ergebnisse der vierten Bundeswaldinventur.

Bundeswirtschaftsminsterium (2022). *germany-s-current-climate-action-status.pdf?__blob=publicationFile&v=1. Federal Ministry for Economic Affairs and Energy - Germany's current climate action status*. [Govenmnet Website]. https://www.bundeswirtschaftsministerium.de/Redaktion/EN/Downloads/E/germany-s-current-climate-action-status.pdf?__blob=publicationFile&v=1 [2026-02-26]

Busch, F.A., Ainsworth, E.A., Amtmann, A., Cavanagh, A.P., Driever, S.M., Ferguson, J.N., Kromdijk, J., Lawson, T., Leakey, A.D.B., Matthews, J.S.A., Meacham-Hensold, K., Vath, R.L., Vialet-Chabrand, S., Walker, B.J. & Papanatsiou, M. (2024). A guide to photosynthetic gas exchange measurements: Fundamental principles, best practice and potential pitfalls. *Plant, Cell & Environment*, 47 (9), 3344–3364. https://doi.org/10.1111/pce.14815

Dusenge, M.E., Madhavji, S. & Way, D.A. (2020). Contrasting acclimation responses to elevated CO2 and warming between an evergreen and a deciduous boreal conifer. *Global Change Biology*, 26 (6), 3639–3657. https://doi.org/10.1111/gcb.15084

European Commission (2023). *Regulation (EU) 2023/839. OJ L*. http://data.europa.eu/eli/reg/2023/839/oj [2026-02-16]

Faria, J.C., Jelihovschi, E.G. & Allaman, I.B. (2015). *Conventional Tukey Test*. UESC.

Farquhar, G.D., von Caemmerer, S. & Berry, J.A. (1980). *A Biochemical Model of Photosynthetic CO2 Assimilation in Leaves of C3 Species*. (Planta, 149). Springer-Verlag.

Ge, Z.-M., Kellomäki, S., Zhou, X., Wang, K.-Y., Peltola, H., Väisänen, H. & Strandman, H. (2011). Effects of climate change on evapotranspiration and soil water availability in Norway spruce forests in southern Finland: An ecosystem model based approach. https://doi.org/10.1002/eco.276

Gebauer, R., Volarík, D., Urban, J., Børja, I., Nagy, N., Eldhuset, T. & Krokene, P. (2018). Effects of mild drought on the morphology of sun and shade needles in 20-year-old Norway spruce trees. *iForest - Biogeosciences and Forestry*, 12 (1), 27–34. https://doi.org/10.3832/ifor2809-011

Gessler, A. & Zweifel, R. (2024). Beyond source and sink control – toward an integrated approach to understand the carbon balance in plants. *New Phytologist*, 242 (3), 858–869. https://doi.org/10.1111/nph.19611

Goisser, M., Geppert, U., Rötzer, T., Paya, A., Huber, A., Kerner, R., Bauerle, T., Pretzsch, H., Pritsch, K., Häberle, K.H., Matyssek, R. & Grams, T.E.E. (2016). Does belowground interaction with *Fagus sylvatica* increase drought susceptibility of photosynthesis and stem growth in *Picea abies*? *Forest Ecology and Management*, 375, 268–278. https://doi.org/10.1016/j.foreco.2016.05.032

Goude, M., Nilsson, U., Mason, E. & Vico, G. (2022). Using hybrid modelling to predict basal area and evaluate effects of climate change on growth of Norway spruce and Scots pine stands. *Scandinavian Journal of Forest Research*, 37 (1), 59–73. https://doi.org/10.1080/02827581.2022.2039278

Grossnickle, S.C. (2000). *Ecophysiology of Northern Spruce Species: The Performance of Planted Seedlings*. NRC Research Press.

Gutierrez Lopez, J., Tor-ngern, P., Oren, R., Kozii, N., Laudon, H. & Hasselquist, N.J. (2021). How tree species, tree size, and topographical location influenced tree transpiration in northern boreal forests during the historic 2018 drought. *Global Change Biology*, 27 (13), 3066–3078. https://doi.org/10.1111/gcb.15601

Guzzon, G., Kühn, N., Hertle, B., Martin, K., Freeth, T. & Sjöman, H. (2026). Evaluating leaf water potential at turgor loss to assess drought tolerance in temperate and Mediterranean shrub species for dry urban environments. *Urban Forestry & Urban Greening*, 120, 129463. https://doi.org/10.1016/j.ufug.2026.129463

Hafner, B.D., Hesse, B.D., Bauerle, T.L. & Grams, T.E.E. (2020). Water potential gradient, root conduit size and root xylem hydraulic conductivity determine the extent of hydraulic redistribution in temperate trees. *Functional Ecology*, 34 (3), 561–574. https://www.jstor.org/stable/48583179 [2026-06-09]

Hafner, B.D., Hesse, B.D. & Grams, T.E.E. (2021). Friendly neighbours: Hydraulic redistribution accounts for one quarter of water used by neighbouring drought stressed tree saplings. *Plant, Cell & Environment*, 44 (4), 1243–1256. https://doi.org/10.1111/pce.13852

Hafner, B.D., Hesse, B.D. & Grams, T.E.E. (2026). Redistribution of soil water by mature trees towards dry surface soils and uptake by seedlings in a temperate forest. *Plant Biology*, 28 (3), 888–896. https://doi.org/10.1111/plb.13764

Hafner, B.D., Tomasella, M., Häberle, K.-H., Goebel, M., Matyssek, R. & Grams, T.E.E. (2017). Hydraulic redistribution under moderate drought among English oak, European beech and Norway spruce determined by deuterium isotope labeling in a split-root experiment. *Tree Physiology*, 37 (7), 950–960. https://doi.org/10.1093/treephys/tpx050

Hagedorn, F., Joseph, J., Peter, M., Luster, J., Pritsch, K., Geppert, U., Kerner, R., Molinier, V., Egli, S., Schaub, M., Liu, J.-F., Li, M., Sever, K., Weiler, M., Siegwolf, R.T.W., Gessler, A. & Arend, M. (2016). Recovery of trees from drought depends on belowground sink control. *Nature Plants*, 2, 16111. https://doi.org/10.1038/nplants.2016.111

Hesse, B.D., Gebhardt, T., Hafner, B.D., Hikino, K., Reitsam, A., Gigl, M., Dawid, C., Häberle, K.-H. & Grams, T.E.E. (2023). Physiological recovery of tree water relations upon drought release—response of mature beech and spruce after five years of recurrent summer drought. *Tree Physiology*, 43 (4), 522–538. https://doi.org/10.1093/treephys/tpac135

Hesse, B.D., Hikino, K., Gebhardt, T., Buchhart, C., Dervishi, V., Goisser, M., Pretzsch, H., Häberle, K.-H. & Grams, T.E.E. (2024). Acclimation of mature spruce and beech to five years of repeated summer drought – The role of stomatal conductance and leaf area adjustment for water use. *Science of The Total Environment*, 951, 175805. https://doi.org/10.1016/j.scitotenv.2024.175805

Hikino, K., Hesse, B.D., Gebhardt, T., Hafner, B.D., Buchhart, C., Baumgarten, M., Häberle, K.-H. & Grams, T.E.E. (2025). Drought legacy in mature spruce alleviates physiological stress during recurrent drought. *Plant Biology*, 28 (3), 637–648. https://doi.org/10.1111/plb.70039

Joseph, J., Gao, D., Backes, B., Bloch, C., Brunner, I., Gleixner, G., Haeni, M., Hartmann, H., Hoch, G., Hug, C., Kahmen, A., Lehmann, M.M., Li, M.-H., Luster, J., Peter, M., Poll, C., Rigling, A., Rissanen, K.A., Ruehr, N.K., Saurer, M., Schaub, M., Schönbeck, L., Stern, B., Thomas, F.M., Werner, R.A., Werner, W., Wohlgemuth, T., Hagedorn, F. & Gessler, A. (2020). Rhizosphere activity in an old-growth forest reacts rapidly to changes in soil moisture and shapes whole-tree carbon allocation. *Proceedings of the National Academy of Sciences*, 117 (40), 24885–24892. https://doi.org/10.1073/pnas.2014084117

Kaiser, H. & Paoletti, E. (2014). Dynamic Stomatal Changes. In: *Trees in a Changing Environment*. (Plant Ecophysiology; 9). Springer Science + Business. https://doi.org/10.1007/978-94-017-9100-7_6

Khadke, L., Verma, A., Mukherjee, S. & Ghosh, S. (2026). Vapor pressure deficit dominates sap flow variability across forest biomes. *Journal of Hydrology*, 664, 134449. https://doi.org/10.1016/j.jhydrol.2025.134449

Kunert, N., Münchinger, I.K. & Hajek, P. (2024). Turgor loss point explains climate-driven growth reductions in trees in Central Europe. *Plant Biology*, n/a (n/a). https://doi.org/10.1111/plb.13687

Lagergren, F. & Lindroth, A. (2002). Transpiration response to soil moisture in pine and spruce trees in Sweden. *Agricultural and Forest Meteorology*, 112 (2), 67–85. https://doi.org/10.1016/S0168-1923(02)00060-6

Lévesque, M., Saurer, M., Siegwolf, R., Eilmann, B., Brang, P., Bugmann, H. & Rigling, A. (2013). Drought response of five conifer species under contrasting water availability suggests high vulnerability of Norway spruce and European larch. *Global Change Biology*, 19 (10), 3184–3199. https://doi.org/10.1111/gcb.12268

Naturvårdsverket (2025a). *Fortsatt reglering av LULUCF-sektorn efter 2030*. (NV-01705-24). Naturvårdsverket.

Naturvårdsverket (2025b). Report for Sweden on projections of greenhouse gas emissions and removals.

Naturvårdsverket (2026). *Sveriges del av EU:s klimatmål*. https://www.naturvardsverket.se/amnesomraden/klimatomstallningen/sveriges-klimatarbete/sveriges-del-av-eus-klimatmal/ [2026-02-26]

Niinemets, Ü. (2002). Stomatal conductance alone does not explain the decline in foliar photosynthetic rates with increasing tree age and size in Picea abies and Pinus sylvestris. *Tree Physiology*, 22 (8), 515–535. https://doi.org/10.1093/treephys/22.8.515

Nilsson, L.O. (1993). Carbon sequestration in Norway spruce in south Sweden as influenced by air pollution, water availability, and fertilization. *Water, Air, and Soil Pollution*, 70 (1), 177–186. https://doi.org/10.1007/BF01104995

Ogana, F.N., Holmström, E., Aldea, J. & Liziniewicz, M. (2024). Growth response of *Pinus sylvestris* L. and *Picea abies* [L.] H. Karst to climate conditions across a latitudinal gradient in Sweden. *Agricultural and Forest Meteorology*, 353, 110062. https://doi.org/10.1016/j.agrformet.2024.110062

Pardos, M., del Río, M., Pretzsch, H., Jactel, H., Bielak, K., Bravo, F., Brazaitis, G., Defossez, E., Engel, M., Godvod, K., Jacobs, K., Jansone, L., Jansons, A., Morin, X., Nothdurft, A., Oreti, L., Ponette, Q., Pach, M., Riofrío, J., Ruíz-Peinado, R., Tomao, A., Uhl, E. & Calama, R. (2021). The greater resilience of mixed forests to drought mainly depends on their composition: Analysis along a climate gradient across Europe. *Forest Ecology and Management*, 481, 118687. https://doi.org/10.1016/j.foreco.2020.118687

Richter, H. (1978). A Diagram for the Description of Water Relations in Plant Cells and Organs. *Journal of Experimental Botany*, 29 (112), 1197–1203. https://www.jstor.org/stable/23689703 [2026-05-19]

Richter, H. & Kikuta, S. (2014). Ecophysiology of Long-Distance Water Transport in Trees. In: *Trees in a Changing Environment*. (Plant Ecophysiology; 9). https://doi.org/10.1007/978-94-017-9100-7_6

Rodriguez-Dominguez, C.M., Carins-Murphy, M.R., Sebastian-Azcona, J. & Brodribb, T.J. (2025). Stem water potential measurements obtained using standard methodologies diverge under extreme drought in tomato and grapevine. *Plant Physiology*, 199 (4), kiaf591. https://doi.org/10.1093/plphys/kiaf591

Schneider, C.A., Rasband, W.S. & Eliceiri, K.W. (2012). *NIH Image to Image J: 25 years of image analysis.* (Nature Methods). https://doi.org/https://doi.org/10.1038/nmeth.2089

Schönbeck, L., Grossiord, C., Gessler, A., Gisler, J., Meusburger, K., D'Odorico, P., Rigling, A., Salmon, Y., Stocker, B.D., Zweifel, R. & Schaub, M. (2022). Photosynthetic acclimation and sensitivity to short- and long-term environmental changes in a drought-prone forest. *Journal of Experimental Botany*, 73 (8), 2576–2588. https://doi.org/10.1093/jxb/erac033

Schulte, L.A., Greiser, C., Eggers, J., Wallin Viman, M., Jarsjö, J. & Schwarz, E. (2026). Spruce volume increases across Sweden – despite decreasing future climate suitable areas. *Scandinavian Journal of Forest Research*, 41 (3), 184–196. https://doi.org/10.1080/02827581.2026.2628636

Silvaboreal - Försök (n.d.). https://www.silvaboreal.com/?p=trial&id=8280 [2026-03-24]

Skogforsk (2026). *Gran (Picea abies). Skogskunskap.se*. [Governement Agency Website]. https://www.skogskunskap.se/aga-skog/fakta-om-skogen/tradslag-i-vara-skogar/gran-picea-abies/ [2026-06-08]

SLU Tönnersjöheden (2025). *Tönnersjöhedens fältstation och försökspark | slu.se*. https://www.slu.se/om-slu/organisation/institutioner/skoglig-faltforskning/forsoksparker-och-stationer/tonnersjohedens-forskningsstation-och-forsokspark/ [2026-02-17]

SMHI (n.D.). *Sveriges klimat. SMHI - Faktapaket Sveriges Klimat.* [text]. https://www.smhi.se/kunskapsbanken/klimat/sveriges-klimat [2026-05-03]

Sommer, P. (2024). *Soil analysis for the roof project in Tönnersjöheden*. boden.art e. U - Ingenieurbüro für Landschaftsplanung und Landschaftsarchitektur.

Svystun, T., Lundströmer, J., Berlin, M., Westin, J. & Jönsson, A.M. (2021). Model analysis of temperature impact on the Norway spruce provenance specific bud burst and associated risk of frost damage. *Forest Ecology and Management*, 493, 119252. https://doi.org/10.1016/j.foreco.2021.119252

Wikberg, P.-E. (2023). *Growing stock for different tree species by Year, County, Table contents, Formally protected areas and Tree species. PxWeb. Official Statistics of Sweden/Riksskogstaxeringen*. [Government Agency Website]. https://skogsstatistik.slu.se/pxweb/en/OffStat/OffStat__AllMark__Virkesforrad/AM_Virkesf_tradslag_1923_tab.px/table/tableViewLayout2/ [2026-06-08]

Zhu, J., Thimonier, A., Etzold, S., Meusburger, K., Waldner, P., Schmitt, M., Schleppi, P., Schaub, M., Thormann, J.-J. & Lehmann, M.M. (2022). Variation in Leaf Morphological Traits of European Beech and Norway Spruce Over Two Decades in Switzerland. *Frontiers in Forests and Global Change*, 4. https://doi.org/10.3389/ffgc.2021.778351

Zhu, S.-D., Chen, Y.-J., Ye, Q., He, P.-C., Liu, H., Li, R.-H., Fu, P.-L., Jiang, G.-F. & Cao, K.-F. (2018). Leaf turgor loss point is correlated with drought tolerance and leaf carbon economics traits. *Tree Physiology*, 38 (5), 658–663. https://doi.org/10.1093/treephys/tpy013

Zweifel, R., Etzold, S., Sterck, F., Gessler, A., Anfodillo, T., Mencuccini, M., von Arx, G., Lazzarin, M., Haeni, M., Feichtinger, L., Meusburger, K., Knuesel, S., Walthert, L., Salmon, Y., Bose, A.K., Schoenbeck, L., Hug, C., De Girardi, N., Giuggiola, A., Schaub, M. & Rigling, A. (2020). Determinants of legacy effects in pine trees – implications from an irrigation-stop experiment. *The New Phytologist*, 227 (4), 1081–1096. https://www.jstor.org/stable/26928224 [2026-02-16]

6. Popular science summary

As anthropogenic climate change progresses, more and more actors across the European Union become interested in forests as a natural storage for greenhouse gases, also referred to as natural carbon sinks. However, recent drought events, like the extreme drought in 2018, have shown how essential sufficient water availability is for trees to be able to uphold their photosynthetic process and thereby growth and carbon sequestration. These drought events, as well as scientific experiments further showed that the long-term growing conditions play a role in photosynthetic activity during drought, which makes them relevant for refining calculations of carbon sink capacity.

This thesis investigates if the growing conditions a tree got accustomed to over several decades, affect their photosynthesis, needle area and shape and their wilting point (turgor loss point) during the first year of a drought. The experiment consists of ten roofs placed around ten mature Norway Spruce and split between a dry higher elevation site and a moist lower elevation site. Ten additional trees function as a control group. Between April 2025 and April 2026 photosynthesis and the opening of the needle's stomata was measured in three field campaigns with a photosynthesis measuring instrument (Li-COR). In April 2026 we also took measurements of the needle's wilting point in Alnarp's laboratories, using an osmometer. More shoots and needles were photographed to measure projected needle area and needle length. Additionally, shoot length and needle dry weight were recorded and the data statistically analysed to see whether the site or the roofs could explain any differences in e.g. photosynthesis, needle length or wilting point.

The results show that those trees which grew on the higher, dry site could keep high levels of photosynthesis relative to those trees on the lower wet site, especially during summer. Similarly, stomatal conductance, a sign of trees conserving water, was higher in those trees on the higher dry site during June, supporting that drought was manageable for the trees in the beginning of summer, despite relative lower water supplies, because they were used to the growing conditions. Furthermore, we observed lower photosynthesis and lower stomatal conductance of roofed trees on the dry, high sites compared to roofed trees on the lower, wet sites, although both sites reduced their gas exchange. This observation indicates that the treatment pushed trees on both wet and dry site into conserving water, despite the trees on high, dry site being used to coping with less soil water.

However, this dynamic reversed in September, when a heavy rainfall relieved the drought stress and the roofed trees showed high levels of photosynthesis, which declined again in April.

Aligning with the photosynthesis, the roofed trees on the dry site had more drought tolerant needles than the roofed trees on the lower, wet site, which confirms that the trees on the dryer sites are more drought resilient than those trees with less time to acclimatise to more frequent dryer conditions. More long-term data is necessary to determine whether trees on either site undergo a physiological adaptation, meaning that they lower their wilting point (π_{tlp}) to protect cell structures. The same pattern was also observable in the stem water potential, another marker of drought stress in a tree.

Lastly, the needle and shoot length did not show an effect from the drought roofs, with shoots of roofed trees on the dryer growing even longer than the generation prior to drought.

In summary, this thesis showed that during the first months of a drought, trees acclimated to drier sites can uphold higher levels of photosynthesis than trees experiencing drought on a wetter site. However, once the drought gets severe enough, even trees acclimated to drier growing conditions will slow down their photosynthesis in order to conserve water. Interestingly enough these trees also exhibited higher drought resilience (more negative π_{tlp}) than roofed trees on the wetter site, whose stem water potential nevertheless started to level with its control group over the course of the year. As we found no evidence of a physiological nor morphological adaptation yet, more long-term data is necessary in order to confidently state when these adaptation processes begin.

Publishing and archiving

Approved students' theses at SLU can be published online. As a student you own the copyright to your work and in such cases, you need to approve the publication. In connection with your approval of publication, SLU will process your personal data (name) to make the work searchable on the internet. You can revoke your consent at any time by contacting the library.

Even if you choose not to publish the work or if you revoke your approval, the thesis will be archived digitally according to archive legislation.

You will find links to SLU's publication agreement and SLU's processing of personal data and your rights on this page:

Every author has to make an agreement, remove or add rows of consent depending on the number of authors. Please remove this text when no longer needed.

☒ YES, I, Esther Lutz, have read and agree to the agreement for publication and the personal data processing that takes place in connection with this

☐ NO, I/we do not give my/our permission to publish the full text of this work. However, the work will be uploaded for archiving, and the metadata and summary will be visible and searchable.