



Effect of drought on Norway spruce volume Increment

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Abstract

Norway spruce is one of the most important species for Swedish forestry. Spruce is sensitive to drought, and it is hypothesized that the tree species will experience frequent drought-induced growth declines under the future climate. This study investigated the impact of drought on the stem growth of Norway spruce, using stem analysis and breast height data collected from two sites in the county of Halland, Southern Sweden. I hypothesized that using breast height data would produce biased estimates compared to the stem analysis data. I found that the stem growth has experienced a reduction under the moderate drought threshold of the SPEI value below -1.31 in May, considering relative growth responses and the SPEI value of -1.23, considering absolute growth responses, based on data combined from the two sites. The results showed that trees have undergone varied recovery years across years following drought years, ranging from one to more than ten years. Further future research is necessary to include more and older trees in the analysis.

Keywords: Stem analysis, Tree rings, Volume increment, breast height.

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Abbreviations

Abbreviation	Description
BH	Breast height
SLU	Swedish University of Agricultural Sciences
SPEI	Standardized Precipitation and Evapotranspiration Index
StemA	Stem Analysis

1. Introduction

From 2011 to 2020, global temperatures were approximately 1.1°C higher than pre-industrial period (1850–1900) and are expected to continue rising, likely reaching 1.5°C above pre-industrial levels in the early 2030s (IPCC,2021). By the end of 21st century, warming is anticipated to increase to around 3–5 °C if greenhouse gas emissions remain high (IPCC, 2021). In Scandinavia, the temperatures have already increased by approximately 1.5–2.5 °C in 2020, and anticipations indicate that it will experience 3–6 °C of warming by the end of the 21st century (IPCC,2021). Such increases will likely result in an increased frequency, duration, and severity of drought, which could fundamentally disrupt the important physiological functions in trees such as water transport and carbon allocation and consequently cause growth reduction or even mortality(Arend et al., 2021; Adams et al., 2017; Anderegg et al., 2012; Ciais et al., 2005; Gupta et al., 2020; Rais et al., 2021; Walthert et al., 2021). The expected changes in precipitation patterns, combined with increasing temperature and atmospheric water demand, make it crucial to understand the species' response to water stress. Norway spruce(*Picea abies*) is both an economically and ecologically important tree species in Europe. In Sweden, Norway spruce comprises approximately 40.3 percent of the standing timber volume (Swedish Forest Agency & Swedish University of Agricultural Sciences, 2020). Nevertheless, its long-term role in the future forestry economy is threatened due to its high susceptibility to drought, particularly when grown on shallow soil with poor water-holding capacity (Rehschuh et al., 2017). It was reported that drought was the major cause of decline across the different parts of Europe, especially after the droughts of 2003 and 2018 (B. Schuldt et al.,2020; Senf et al.,2020). This is particularly evident in southern Sweden, where Norway spruce was found to be the most drought-susceptible tree in recent years (Aldea et al., 2023; Ogana et al.,2024). Growth decline driven by reduced soil moisture and increased air temperatures has been reported by multiple studies, indicating that water stress limits the spruce growth by altering the physiological process (Karlsson et al.,2023; Aldea et al.,2022). Radial growth decline of Norway spruce has been quantitatively associated with drought-driven soil moisture deficit, with prolonged periods of low soil moisture strongly reducing the stem basal area increment (Karlsson et al.,2023). Nevertheless, previous studies have analyzed the effect of drought on Norway spruce growth in southern Sweden; most have mainly relied on stem measurements taken only at dbh, rather than collecting data from multiple heights along the stem (Karlsson et al., 2023; Tufvesson, 2018). Moreover, these studies often relied on data that were not resolved at the annual scale. Together, these limitations restrict the ability to assess how drought influences stem growth,

leaving drought effects on Norway spruce in Southern Sweden only partially understood.

There are various drought indices that are widely used to assess the drought impact on the forest growth, including the Standardized Precipitation Index (SPI) and the Palmer Drought Severity Index (PDSI) (McKee et al., 1993; Palmer, 1965). However, SPI solely considers precipitation anomalies, ignoring temperature, vapour pressure deficit, and evapotranspiration, and PDSI considers both but fails to reflect the short-term droughts (Vicente-Serrano et al., 2010). Instead, the standardized Precipitation- Evapotranspiration index (SPEI) was developed to include the effects of temperature, and considering multi-timescale analysis starting from 1,3, 6,12, 24 months or even more (Vicente-Serrano et al., 2010).

It is of high importance to provide reliable estimates of drought effects on volume growth, as these estimates shape the future management and development of forests and drive sustainable productivity.

Estimation of drought effects on the growth of trees can be achieved by two proxies. 1) Stem analysis involves measuring the volume growth using data collected from multiple heights along the stem, where trees within sites are destructively harvested, prepared, measured, and analysed to generate volume increments. 2) Allometric equations use data collected at dbh (radial growth) to obtain volume increments. The stem analysis method is considered the most accurate approach for assessing the effects of drought on growth. However, destructive sampling is time-consuming, labor-intensive, and not allowed in certain areas or on species that are under protection. Allometric equations are therefore used for assessing the volume dynamics to avoid the drawbacks of stem analysis. Allometric equations, as well as increment cores data collected at dbh, are preferred and widely used, especially in Europe. However, this approach is considered less accurate because it assumes that radial growth at the breast height represents growth dynamics of the entire tree, while studies on other tree species show that growth responses vary along the stem (Longuetaud et al., 2017; Metsaranta, J. M., & Bhatti, J. S., 2016). This study assessed the effects of drought on volume growth of Norway spruce in Southern Sweden, using data collected at multiple heights along the stem (Stem analysis) to ensure reliable estimation. I put forward the following questions:

- (1) What level of drought triggers the decline?
- (2) By how much can drought reduce growth?
- (3) What's the duration of the drought-induced decline?

2. Materials and methods

2.1. Site description and sample collection

The data were collected from two sites (SIS, S25) located at Tönnersjöheden (56° N, 13° E), an experimental forest managed by the Swedish University of Agricultural Sciences (SLU) and situated in the hemiboreal zone near the Atlantic coast in the southern Sweden (Figure 1). The sites are distributed at elevations ranging from 100 m to 132 m above sea level, in a maritime climate characterized by mild temperatures and high precipitation. For the reference period 1961–1990, the mean annual air temperature was recorded to be 6.4 °C, and the mean annual precipitation was 1053 mm (Alexandersson et al., 1991). The duration of the growing season, defined by temperatures greater than 5 °C, is 204 days (Olsson and Staaf, 1995).

The sampled plots consisted of even-aged monoculture stands of Norway spruce. Destructive sampling was conducted, and a total of eight spruce trees were collected: five from site S25 and three from site SIS. Entire cross-sections were extracted at the ground level, breast height (1.3 m above the ground), and then at 2-m intervals along the main stem until the stem diameter fell below 5 cm. Tree height and crown height were measured using a measuring tape after the tree was felled. Each cross-section was labeled with a pencil, indicating the species, site, and tree number and height of the sampling before being transported to the dendrochronological laboratory for analysis. Samples were mounted on wooden cores using water-soluble glue and stored in paper bags to dry at ambient temperature for several days (Cherubini et al., 2020). Thereafter, samples were sanded to make the rings clearly visible.

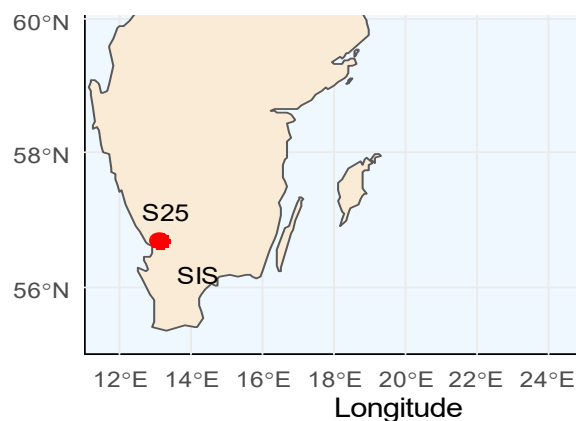


Figure 1. Location of the experimental sites where trees were sampled. Tönnersjöheden (SIS, S25).

Table 1. Site characteristics of the studied spruce stands.

Site ID	Longitude	Latitude	No.Trees	Age
S25	13.07	56.69	5	48,53,50,48,51
SIS	13.10	56.68	3	52,51,51

2.2. Data preparation and building of tree ring chronology

The cross-sections were scanned at a resolution of 2400 dpi using an Epson Perfection V600 scanner. The tree rings were cross-dated and measured to an accuracy of 0.01 mm using CooRecorder and the CDendro 9.1 program by Cybis™ (Cybis Elektronik & Data AB, 2018). The resulting tree ring width series (RWIs) were stored in the decadal (Tucson) format. Those data were imported into the R environment, where they were screened for completeness and consistency, using the R library `dplR`.

For response function analysis, I detrended the ring-width series to remove biologically related trends and other non-climatic signals. Detrending was performed using the spline function from the dendrochronology program library in R (`dplR`) (Bunn, 2008), with the smoothing parameter set to a 50% frequency response at 32 years. The detrended series (ring-width indices, RWI) were then pre-whitened using auto-regressive moving average modelling to remove serial autocorrelation and thereby improve the “common signal” and ensure each year’s ring width is independent (Cook & Kairiukstis, 1990). Afterwards, individual ring-width indices for each site were combined and averaged to produce a site chronology using Tukey’s bi-weight robust mean, representing the mean growth pattern shared among trees at the site (Cook & Kairiukstis, 1990). Importantly, detrended indices were not used to compute growth loss metrics, which relied on absolute growth values.

2.3. Climatic data and identification of extreme drought events

The climate data used in this study were downloaded from the ERA5 European reanalysis (Hersbach et al., 2020). Monthly records of temperature, dew point, shortwave radiation, wind components, and precipitation were extracted from NetCDF files using the R package *terra* (Hersbach et al., 2020; Hijmans, 2023). Since the two sites used in the study were located within 10 km of each other, they were represented by identical sets of climate data.

The downloaded variables were subsequently used to calculate the potential evapotranspiration (PET) using the Penman-Monteith equation (Allen et al., 1998). The PET was then subtracted from the total evapotranspiration to derive

the water balance, which served as the basis for computing the Standardized Precipitation Evapotranspiration Index (SPEI) at two month scale. This was computed by the R package *SPEI* (Vicente-Serrano et al., 2010). SPEI was calculated for the period 1960–2024. Negative SPEI values indicate dry conditions, while positive values indicate moist conditions. As the growing season for spruce is May to June (Zhang et al., 2016), I then selected the SPEI series from May to June for further analysis. The negative abnormal SPEI values were identified and were marked as extreme drought years, with 1992 being the most severe drought year. Each drought year was treated as a discrete disturbance event, and further analysis was centered on these drought years to assess growth decline and recovery dynamics.

2.4. Growth-climate relationships

To analyze how the tree-ring chronologies relate to climatic conditions, I performed response function analysis implemented in the R package *treeclim* (Zang & Biondi, 2015). The method quantifies the influence of multiple intercorrelated climate variables upon standardized ring width indices while controlling for multicollinearity, to allow precise and stable estimates of regression coefficients and their statistical significance. The response functions were obtained by considering monthly temperature and SPEI data as climate predictors and index chronologies as the predictand variables. Simple correlation coefficients between ring width indices and climate variables were calculated to produce correlation functions. The analysis used the period spanning from March to August of the current year. The statistical significance of climate variables was verified with the bootstrap method by the R package *bootRes* that estimates the 95% confidence intervals of the regression coefficients in response functions (Biondi, 1997). For each site, I then identified the important climatic variable (i.e., SPEI) based on the relationship between growth indices and SPEI.

2.5. Calculation of Volume Increment

2.5.1 Stem analysis volume estimates

To conduct stem analysis and obtain annual volume increment chronologies for each sampled tree, I used the *stemAnalysis* function (R package *treeglia*) (Bascietto M, 2007) in the R program, an approach that combines annual ring width measurements extracted from multiple heights on the stem. First, the annual rings of each cross-section were cumulatively summed from the pith to the bark to reconstruct the dynamics of the annual radius of the stem. This produced a time

series of historical radii, indicating the diameter of the tree at that height for each growth year. Using these reconstructed radii, the basal area of the cross-section at each height was calculated:

$$G = \pi \cdot (w)^2.$$

Where G is the basal area of cross-section, and w is the radius of cross-section.

Second, because the height of the tree at the point of sectioning underestimates the actual height at the presumed age, as the true height growth occurs at some point above the cross-section (hidden tip), the actual annual height growth was obtained using the Carmean interpolation (Carmean, 1972). This algorithm estimates past tree heights by interpolating height increments between successive stem sections based on their relative positions and ring counts.

Third, the stem was segmented into logs defined by consecutive cross sections. The annual volume growth was calculated using Smalian's formula (Husch, Beers, & Kershaw, 2003):

$$V_i = \left(\frac{G_i + G_{i+1}}{2} \right) \cdot (h_{i+1} - h_i)$$

Where, V_i is the volume of individual log enclosed between i^{th} and $(i + 1)^{th}$ cross sections, G_i is the basal area of i^{th} cross section, G_{i+1} is the basal area of the $(i + 1)^{th}$ cross section, h_i is the height of the i^{th} cross section and h_{i+1} is the height of $(i + 1)^{th}$

This formula assumes logs are frustums with parallel cross-sections and estimates the volume over time. For the highest cross-section, the volume is calculated in a conical approximation, which assumes the stem tapers smoothly to the tip. Fourth, the total annual volume was obtained by summing the volume of all logs and the volume of the cone formed by the highest cross-section and terminal bud:

$$V = \sum_{i=1}^n v_i + \frac{G_n}{3} \cdot (h_{tree} - h_n)$$

Where V is the total annual volume, V_i is the volume of individual log, G_n is the basal area of cross section, h_{tree} is the total height of the tree, and h_n is the height of cross section.

Lastly, the annual volume increment was computed by subtracting the subsequent volume pools and was referred to as Observed Volume Increment (OVI):

$$VI = V_y - V_{y-1}$$

Where VI is the total volume increment, V_y is the total volume at a certain year, and V_{y-1} is the total volume of the previous year.

While the stem analysis-based estimates were considered the true standard for comparison with alternatives derived from the breast height sample, they are not entirely free from uncertainty. The differences can arise from the method used to interpolate height between cross sections (Blackman et al., 2019), the choice of standard model to calculate log volume (Skelton et al., 2025; Tangjialeke et al., 2024), the number of cross-sections sampled and the number of radii measured for each sample (Breda et al., 2006), and the fact that trees are not perfectly circular in cross section (Tangjialeke et al., 2024; Skelton et al., 2025).

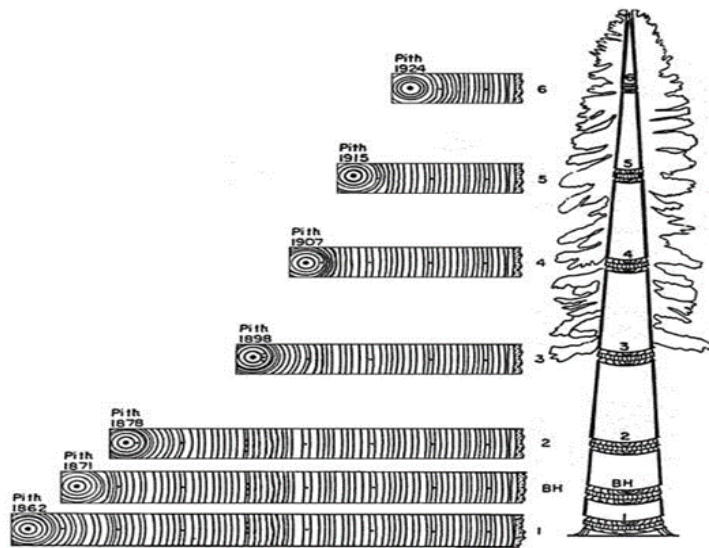


Figure 2. The sampling scenario of cross-sectional discs obtained from individual trees. Credit: <https://teagasc.ie/news--events/daily/how-can-we-decipher-the-effects-of-climate-change-in-t>

2.6. Assessment of volume loss

I estimated the volume loss as the departure between observed tree growth and expected tree growth. Considering the availability of climatic information spanning from 1940 to 2024, I quantified the effect of all drought years that occurred in that period (McKee et al. 1993). SPEI was also used to predict tree growth after each drought year. For each drought year, the Pre-drought period was defined as all years preceding that year. Since the volume growth of each tree in the pre-drought period followed its individual growth trajectory, I modeled the expected future growth of the tree using only the pre-drought dynamics of that same tree, rather than relying on control trees. This allowed comparisons between observed post-drought growth (OVI) and the projected growth trajectory (PVI). To achieve this, I fitted a polynomial regression function with two degrees of freedom (Zuur, Ieno, & Smith, 2007). Observed and projected growth were then summed over different time periods, including six years of post-drought years, the

period from the drought year to the time of sampling, and a dynamically defined decline–recovery interval. This cumulative approach integrates multi-year growth responses and captures both immediate and delayed effects of drought.

I defined the timing of growth recovery as the year (later referred to as *recovery year*), when the observed growth reached 95% or above of the projected growth. The duration of the recovery period was defined as the period between the drought year and the recovery year. For each sampled tree, I estimated the total volume loss after drought by comparing the observed volume increment (OVI) with the projected volume increment (PVI) over the decline period. I calculated the relative growth response by computing the ratio between OVI and PVI, and I obtained the absolute growth response by subtracting the OVI from the PVI. Specifically, I used the following formulas:

$$VL_{PVI} = \sum \left(\frac{OVI}{PVI} \right)$$

$$VL_{PVI} = \sum(OVI - PVI)$$

The Relative growth responses are considered more realistic because they express growth relative to each tree’s expected performance, thereby accounting for differences in tree size and growth potential.

2.6.1. Threshold analysis

To quantify the level of drought that triggers decline, I performed threshold analysis (Fig.4). I identified three driest years, acknowledging that some years were not really drought years. However, I needed them to expand the gradient of drought conditions toward less extreme conditions, making it possible to clearly identify the drought level linked to growth decline. I then identified the threshold at which observed volume growth was significantly lower than expected from the projection data. To achieve this, I regressed growth responses against SPEI using polynomial regression fitted separately to the individual tree using that tree’s annual volume growth response data derived from the previous section (*Assessment of volume loss*). The threshold was defined as the SPEI value at which the fitted mean response crossed the neutral response line.

2.6.2. Growth Response Analysis by Site

Both relative and absolute growth response of trees at the two sites during the driest year were compared (Fig 5&6). To visualize differences between the sites,

boxplots were created showing the medians, interquartile ranges, and variability of growth responses. To statistically evaluate differences between the two sites, an independent two-sample t-test was performed.

2.7. Defining the decline period

I defined recovery year as the year when the tree returned to the expected growth trajectory, i.e., when the differences in growth dropped below 5 % (Fig.7). The interval between impact and recovery years was defined as the decline period. If observed growth never returned to projected levels, recovery was considered absent, and its duration was estimated as the difference between the event year and the date of the last ring on the sample, providing a conservative estimate of decline duration. I particularly analyzed the decline period beyond 1992 as the most severe drought year for each tree.

3. Results

3.1. Site-specific climate-growth relationship

The response function analysis revealed differences in climate sensitivity of spruce between two sites (Fig. 3). At SIS, growth exhibited only weak, non-significant correlations with temperature. In contrast, temperature in March positively affected growth at S25. On the other hand, the SPEI in May showed a significant positive correlation with growth at SIS, whereas at S25, I did not observe significant correlations of growth with SPEI.



Figure 3. Results of response function analysis operating on ring width indices (RWI) and monthly mean temperature (blue color), and Standardized Precipitation Evapotranspiration Index (red color). Solid lines indicate significant correlations ($p < 0.05$), whereas dashed lines denote non-significant relationships.

3.2. Volume loss estimates

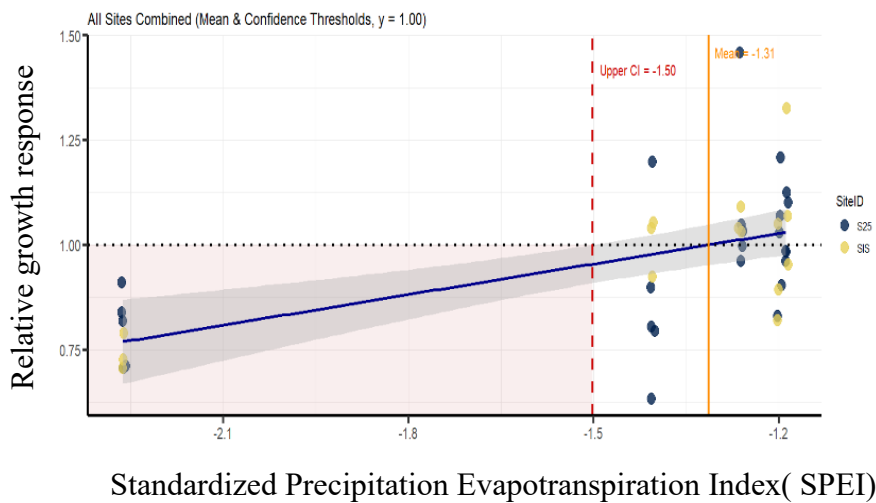
3.2.1 Threshold analysis

The relative tree growth response indicated that growth decline was less pronounced with less severe drought, as reflected by the overall positive slope of the fitted curve (Fig 4a). The figure shows that growth declined under moderate drought conditions, with the SPEI reaching a threshold of -1.31, whereas more pronounced growth reductions occurred under more severe drought conditions

around a SPEI value of -1.50. Some particular trees exhibited comparable growth reductions at SPEI values of -1.4 and -2.2.

Fig 4b shows the growth response in terms of absolute volume increment and similarly indicates that growth decline became less pronounced with less drought severity as reflected by the positive slope of the fitted curve. Growth declined under moderate drought, with a mean threshold SPEI value of -1.23, while a more pronounced decline occurred under severe drought conditions at a SPEI value of -1.39. Some trees lost the same amount of volume at -1.3 as at -2.2, indicating that responses vary considerably among individual trees.

A)



B)

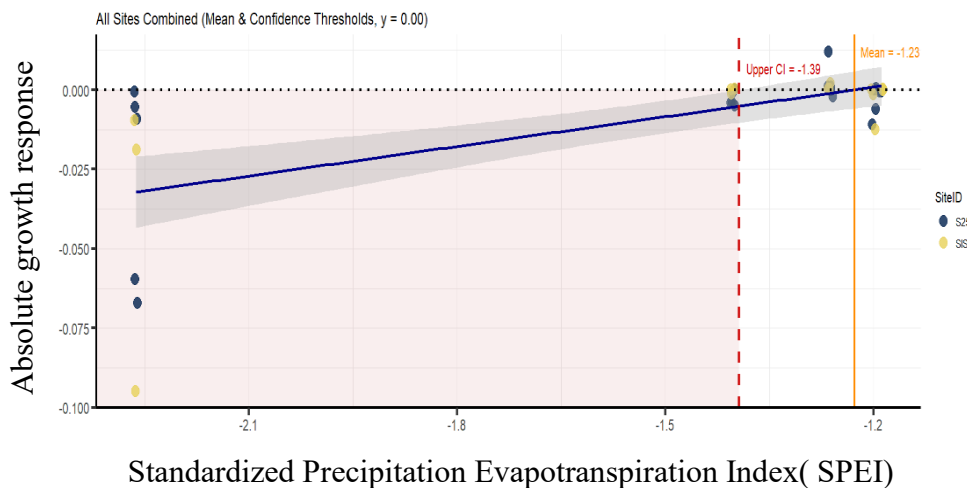


Figure 4. Relationship between spring (May–June) Standardized Precipitation Evapotranspiration Index (SPEI; X-axis) and tree growth: growth ratio in panel (a) and absolute increment in panel (b) (Y-axis). Each colored point represents a tree–drought year combination. The blue line shows a fitted non-linear smoothing curve, with the 95% confidence band indicated in gray. The dotted horizontal line represents no growth

response. The orange line indicates the threshold at which growth decline begins, while the dashed red line denotes the threshold for pronounced growth decline.

3.2.2. Growth Response Analysis by Site

The boxplot analysis of relative growth response shows that the median growth at S25 (0.82) was slightly higher than that at SIS (0.7) (Fig. 5). S25 exhibits a wider interquartile range than SIS, indicating higher variability in growth responses among the trees at S25. In contrast, the interquartile range at SIS is more clustered, signifying consistent growth responses among trees. The whiskers display comparable ranges of growth responses to drought, with two outliers at S25, one showing particularly high growth and the other showing the lowest growth, similar to one outlier at SIS. However, the results of the t-test ($P = 0.2$) indicate no significant difference between the sites (Table.2).

This pattern is even more evident in the analysis of growth responses on an absolute scale (Fig. 6), where the median values are closer, and the interquartile ranges and whiskers show greater overlap. The analysis also reveals that one tree at SIS experienced a particularly pronounced growth decline. Similarly, the results of the t-test ($P = 0.7$) confirm that there is no significant difference between the sites (Table.3), indicating that the observed differences in median growth could be due to random variation

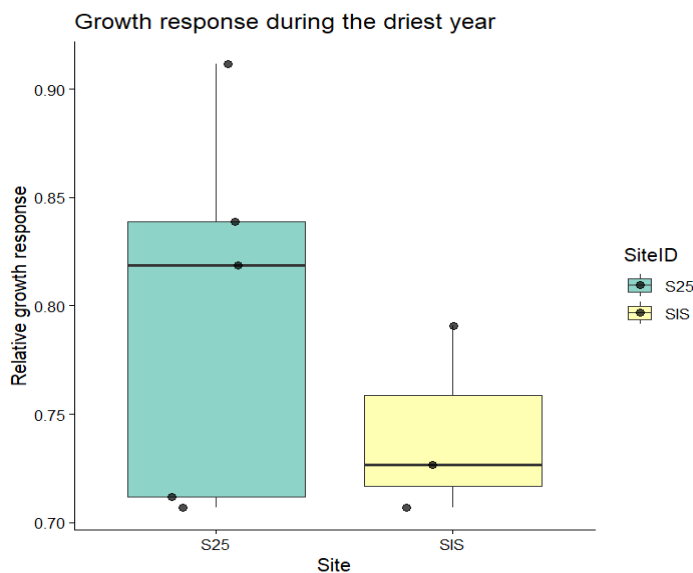


Figure 5. Boxplots showing drought-induced growth responses of spruce on a relative scale at sites S25 and SIS. The green and yellow boxes represent the interquartile range (25th–75th percentile) with the median indicated by the thick horizontal line. The black vertical lines are whiskers that show the overall range of growth responses, and black dots denote individual trees.

Table 2. Descriptive statistics of drought-induced growth on the relative scale for sites S25 and SIS

Site	N	Mean growth	Standard deviation	Standard error	p-value
S25	5	0.79	0.08	0.0362	0.2
SIS	3	0.74	0.04	0.02	

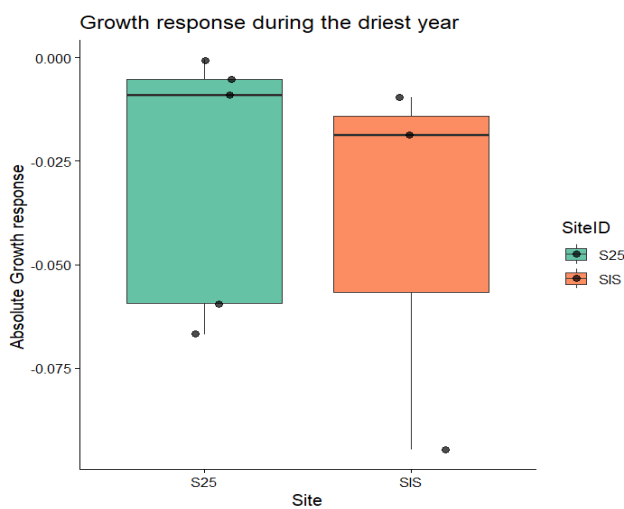


Figure 6. Boxplots showing drought-induced growth responses of spruce on an absolute scale at sites S25 and SIS. The light blue and light green boxes represent the interquartile range (25th–75th percentile) with the median indicated by the thick horizontal line. The black vertical lines are whiskers that show the overall range of growth responses, and black dots denote individual trees.

Table 3. Descriptive statistics of drought-induced growth on an absolute scale for sites S25 and SIS.

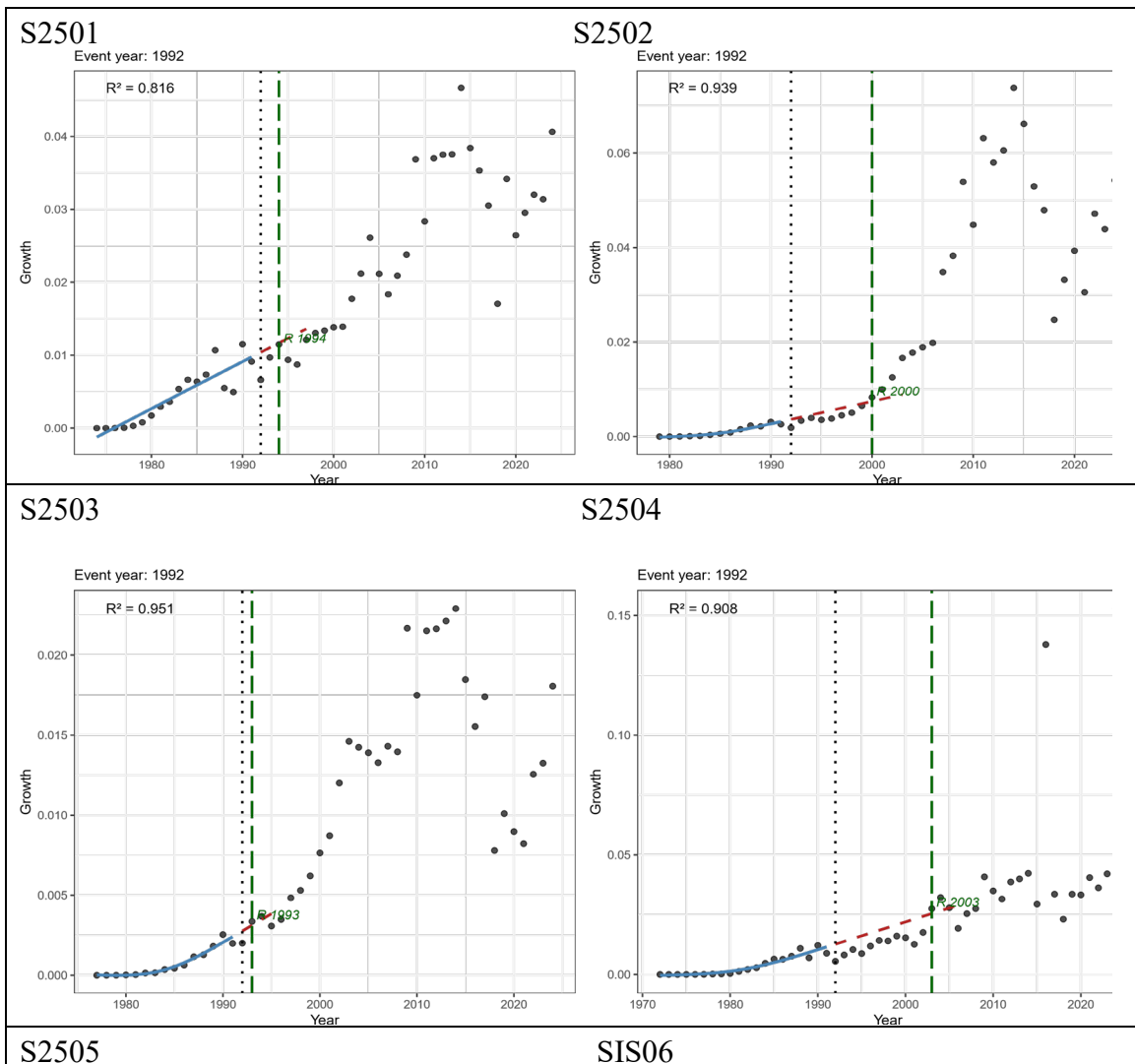
Site	N	Mean growth	Standard deviation	Standard error	P-value
S25	5	-0.028	0.032	0.014	0.7
SIS	3	-0.041	0.046	0.027	

3.3. Decline Period and Recovery

Following the 1992 drought year, the observed growth of tree S2501 fell below the projected growth trajectory, indicating an evident drought-induced decline. This decline lasted only for two years, as the recovery occurred by 1994.

Similarly, for S2502, there was a growth decline after the event year. However, this decline lasted a bit longer as growth recovered to the expected level by approximately 2000, corresponding to a recovery period of six years. For S2503, the growth decline was the most short-lived, as the recovery happened in only one year, indicating the high resilience of this individual tree against drought.

For trees S2504 and S2505, growth recovered by 2003, indicating a much longer decline period and an extended recovery phase of about 10 years. In the case of SIS06, growth recovered by 1999, equivalent to a six-year recovery period. SIS07 showed recovery only by 2011, demonstrating a markedly prolonged decline with a recovery period of nearly 20 years. SIS08 recovered by 1998, indicating a recovery duration of approximately six years.



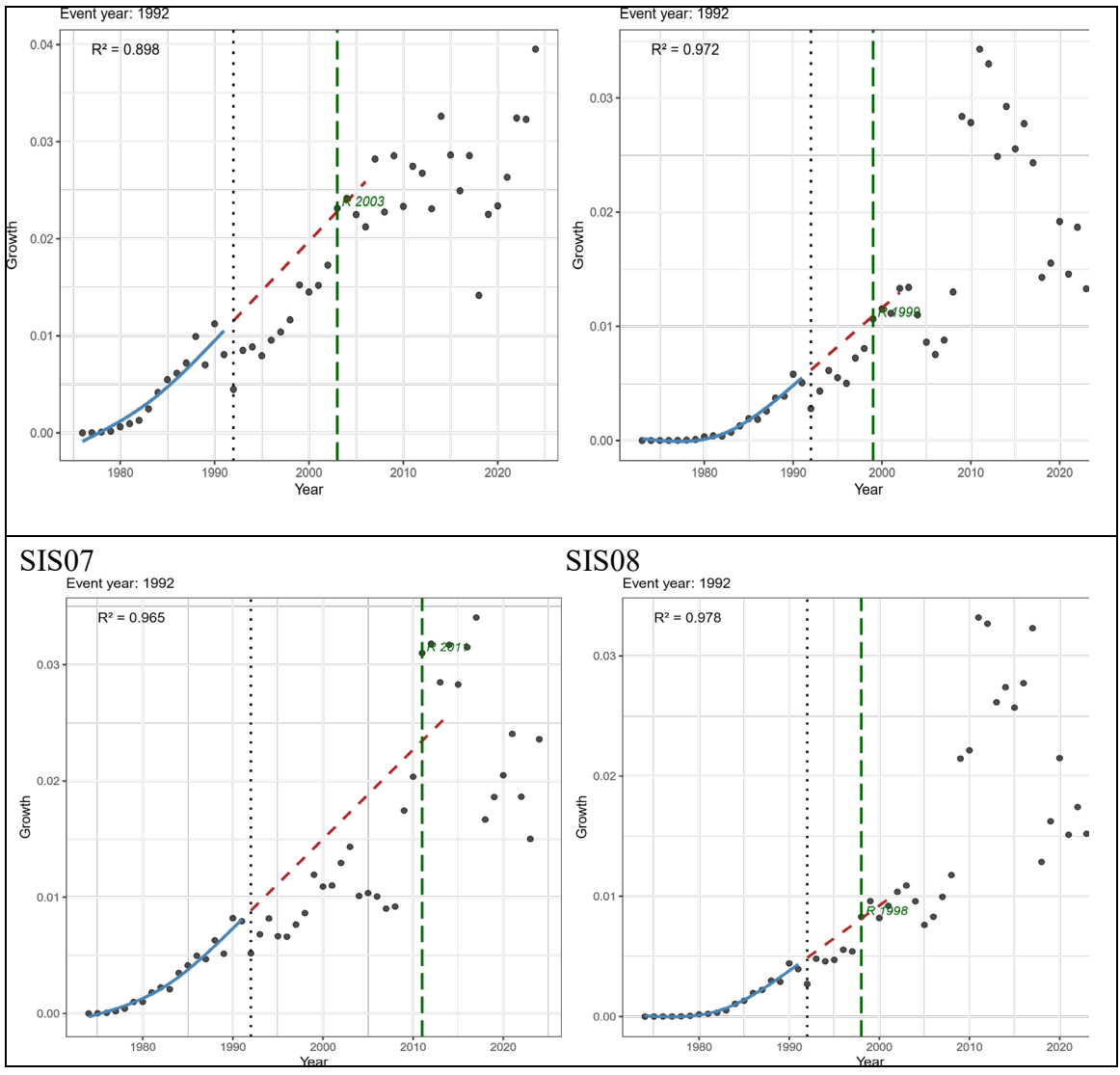


Figure 7. Growth responses of individual trees following the 1992 drought event. Black dots represent observed annual growth, the red dashed line indicates the projected (expected) growth trajectory based on the fitted model, and the blue line shows the pre-event growth trend used for model calibration. The vertical black dotted line marks the drought event year (1992), while the green dashed vertical line denotes the identified recovery year

4. Discussion

This study evaluated the impact of drought on Norway spruce volume increment. Across 8 trees from two plots, I showed the effects of SPEI and temperature on the growth of the species. By using data from stem analysis and those from breast height function, I evaluated the growth responses of species to climatic conditions. The hypothesis that breast height-based volume growth estimates are biased was not supported by the results.

4.1. Climate- growth relationship

Although both sites are geographically close and located at similar elevations, they exhibit partially different responses to climate when analyzed at the monthly scale. These differences may be influenced by factors such as canopy openness, which affects light penetration, evaporation demand, and soil drying rates (A. Lenk et al., 2024). The results indicate that the volume growth of Norway spruce correlates positively with SPEI in late spring (May) at SIS (Fig. 3), highlighting the critical role of water availability in tree growth. This finding aligns with previous studies showing that increased moisture in late spring enlarges cells and promotes growth (Pandey, J., Wood Sci., 2021).

However, at S25, SPEI did not have a measurable influence on growth, whereas temperature in early spring (March) positively influenced growth, reflecting the role of warmer conditions in reactivating cambial activity after winter dormancy (Miller, T. W., et al., 2020). While this study finds no correlation between growth and climatic conditions in the late summer months, earlier research suggests that favorable thermal conditions in June can accelerate cambial activity, boosting growth through enhanced photosynthesis, carbohydrate availability, and metabolic rate (Nilsson, Ö., et al., 2019; Popa, A. et al., 2024). Conversely, other studies report that high summer temperatures can reduce growth due to increased evapotranspiration and water stress (Aldea et al., 2022; Pretzsch et al., 2018)

4.2. Degree of growth decline

The relative growth response analysis showed that growth was generally influenced by drought intensity. The positive slope of the fitted curve indicates that growth decline became less pronounced with less drought severity (Fig.4a). A similar pattern was observed in the absolute increment analysis (Fig.4b). The relative growth responses indicate that growth accumulated as expected until reaching a mean SPEI threshold of -1.31 (moderate drought), after which growth began to decline. The decline became more pronounced at an SPEI value of

-1.50. For the absolute growth increment, the threshold for growth decline occurred slightly earlier, at a SPEI value of -1.23, with a more pronounced decline observed below -1.31. Both approaches indicate broad sensitivity of spruce to moderate and even severe drought conditions. These findings are consistent with previous studies highlighting water availability and favorable soil conditions as key limiting factors for growth accumulation (Rabbel et al., 2018; Waring and Running, 1998; Bréda et al., 2006). However, variability among individual trees was evident. Some trees exhibited similar growth reductions under extreme drought conditions (SPEI -2.2) as others did under less severe drought (SPEI -1.4), and this was clearly indicated by growth response analysis by sites (Fig 5), where trees have shown higher growth variability, especially at the S25 site. This variability indicates that neighboring stands or individual trees may occupy different positions relative to their physiological drought limits despite experiencing the same drought events. This interpretation aligns with findings from Meinzer et al. (2016) and Blackman et al. (2019), which emphasize that traits such as xylem vulnerability, turgor loss point, and stomatal regulation strategies strongly influence drought susceptibility. Trees operating closer to their hydraulic failure thresholds are more vulnerable than those with greater hydraulic safety margins. The fact that sites or individual trees respond differently to drought conditions highlights the importance of fine-scale site characterization when assessing forest vulnerability. A particular stand or tree may function as a local refugium under increasing water stress, while a nearby stand or tree may face an increased risk of growth decline. However, in my case, growth response analysis by site indicates that there are no significant differences between the two sites, suggesting that site-specific conditions did not have a measurable influence on drought-induced growth decline.

4.3. Duration of the decline period and recovery

This study identified three severe drought events that occurred throughout the lifespan of the studied trees, and it examined the length of the growth decline period they caused. Relying on 1992 as the most severe drought year, the studied trees have been found to experience a varied duration of the decline period, indicating substantial heterogeneity in drought sensitivity. While some trees exhibited prolonged decline that lasted up to more than ten years, others experienced short decline periods that lasted one to six years (Fig.7). This reflects micro-site conditions and tree-level traits such as rooting depth, hydraulic architecture, and stand-level interactions (Zavadilová et al., 2023; Kurjak et al., 2012; Bolte et al., 2010).

In all cases, there was growth recovery, which means that the observed drought did not lead to permanent decline/mortality. When the drought becomes severe,

the research shows two abiotic mechanisms, i.e., carbon starvation and hydraulic failure, as the main causes of growth decline and mortality under drought (Adams et al. 2017; Hartmann 2011; McDowell et al. 2008, 2019; Sevanto et al. 2014). Those mechanisms can occur in combination or relate to each other in some way (Adams et al. 2017). Conservative Isohydic physiological properties of spruce are one of the factors that enable it to withstand dry conditions. This is due to its ability to close the stomata during dry seasons, reducing transpiration (Zavadilová et al., 2023; Juráň et al., 2023). However, this mechanism creates a trade-off as it can cause carbon starvation, which can also be associated with hydraulic dysfunction from the high hydraulic vulnerability of xylem. Together, those mechanisms reduce carbon uptake and photosynthetic activities, which consequently lead to growth decline and mortality as well (Zavadilová et al., 2023; Ditmarová et al., 2010; Leuzinger et al., 2012; Krejza et al., 2022). This is possibly why, in some cases (trees with more than 10 years of recovery period), growth was unable to recover quickly when the tree regained water (Choat et al. 2018; Wu et al. 2018). The presence of a tree with short-lived growth decline of one year further indicates the role of inherent resilience and favorable local conditions, and emphasizes that spruce growth response to the drought is non-linear and variable.

Limitations and Future Research

I encountered two limitations in this study. First, a low sample size in a particular age class may have affected the estimation of the decline period and the assessment of the duration between the drought event and the sampling date. Second, specific management history towards sites was missing, which may have influenced physiological functions and affected how tree growth reacts to the disturbance. I recommend that future research should consider a bigger sample size across multiple sites with different ages, test age as a fixed effect, and include management records. Those improvements would contribute to more reliable and generalized findings.

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Popular science summary

Frequent and severe drought conditions affect the physiological functions of trees, causing growth decline and even mortality. Norway spruce is an ecologically important species in Sweden that has frequently been reported to be affected by drought.

This study assessed the effects of drought on Norway spruce in terms of volume increment. Using data obtained from multiple heights along the stem, I examined how both temperature and water availability influence growth and the recovery trajectory following drought-induced decline.

Water availability is the critical factor influencing growth. Droughts in late spring caused a significant growth decline, while temperature alone had no effect during that period. Sites experienced growth decline at different drought thresholds. However, growth responses did not differ significantly among sites, but they did vary among individual trees. Recovery periods also varied widely among individual trees, ranging from one year to more than ten years.

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