Drought effect on oak growth:

quantifying losses in volume increment across Southern Sweden

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Torkans effekt på eken: Hur mycket volymtillväxt förlorar vi i Sydsverige?

Mateusz Muzolf

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Abstract

Climate change has increased the frequency and intensity of droughts, negatively affecting growth and productivity of trees such as pedunculate oak (*Quercus robur* L.), which is an important species in Sweden from both economic and ecological perspectives. Although current abundance of the species is strongly reduced, predictions of the future distribution indicate northward expansion of its range under climate change scenarios.

In this study I quantified oak volume growth responses to drought in Southern Sweden, focusing on climatic drivers, sensitivity analysis, recovery dynamics and comparison of two methods assessing the growth response.

Oak growth was mainly driven by water availability, showing significant responses to Standardized Precipitation Evapotranspiration Index calculated over three-month period (SPEI3) in spring and early summer, while temperature effects were weak and inconsistent. Growth response varied among trees and sites, but oak showed relatively high resistance to water stress. Recovery of oak growth occurred typically within one year after the drought, showing high resilience of oak to climatic variability. Growth responses were consistent along the stem, indicating that growth was reduced uniformly at different stem heights.

Keywords: Pedunculate oak, growth response, drought, volume increment

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Abbreviations

Abbreviation	Description
dbh	Diameter at breast height (1.3 m)
Δdiv	Relative growth response (observed / projected growth)
Δsub	Absolute growth response (observed – projected growth)
SPEI	Standardized Precipitation Evapotranspiration Index

1. Introduction

Climate change and drought in forests

The role of climate change in affecting forest ecosystems increases worldwide. Rising air temperatures together with changed rainfall patterns lead to increase in frequency, duration and intensity of drought events (Allen et al., 2010; IPCC, 2023). Drought limits tree growth and productivity in forest ecosystems by reducing available water for plants. Water stress affects physiology of trees by reducing photosynthetic activity and constraining carbon assimilation. As a result, drought conditions lead to reduced shoot elongation (Lobo-do-Vale et al., 2019), diameter and height growth (Van Kampen et al., 2022), and may accelerate leaf senescence and increase probability of crown dieback (Frei et al., 2022) which limit leaf area and reduce photosynthesis even more. Prolonged droughts reduce the period with suitable conditions for growth by shortening the growing season (Lobo-do-Vale et al., 2019). Reduced growth at tree level leads to lower productivity at the stand and ecosystem level (Holm et al., 2023; Itter et al., 2017; Reyer et al., 2014). Growth responses of forests may depend on stand age, density, and species composition (Benisiewicz et al., 2024; Itter et al., 2017; Zuidema et al., 2025).

Drought definition and droughts in Sweden

Drought can be defined as a temporal water deficit, occurring when atmospheric evaporative demand is higher than precipitation. Standardized Precipitation Evapotranspiration Index (SPEI) is a commonly used measure to quantify drought severity. It integrates both precipitation and evaporative demand, which is driven by temperature into a standardized index (Vicente-Serrano et al., 2010). Drought severity thresholds applied to SPEI are usually adapted from those developed for SPI (Standardized Precipitation Index). SPEI values of ≤ -1, ≤ -1.5 and ≤ -2.0 indicate respectively moderate, severe and extreme drought (Mckee et al., 1993; Wang et al., 2014).

Droughts occur relatively frequently in Swedish forests. The most severe recent events here were observed in 1976, 1992, 2003 and 2018. Recent study showed that frequency and intensity of droughts increased during last decades (Laudon et al., 2024). An extremely severe drought was observed in 2018 and it resulted in widespread reductions in forest vitality and growth across Sweden (Wilcke et al., 2020). It also triggered bark beetle outbreaks, leading to extensive tree mortality and a decrease in tree productivity (Knutzen et al., 2025). Earlier, in 2003 drought had similar effects (Teutschbein et al., 2022). Combined very long-lasting heatwave with water deficit caused noticeable decline in forest productivity and

associated changes in regional carbon balance (Ciais et al., 2005; Vitasse et al., 2019).

Pedunculate oak in Europe and Sweden

Pedunculate oak (*Quercus robur* L.) is one of the most important broadleaved tree species in Europe from both economic and ecological perspectives. The species exhibits high production potential and provides quality wood with broad range of use (Krutovsky et al., 2025; Scharnweber et al., 2013; Spiecker, 2021). Large and old oaks also play an important role in forest biodiversity by supporting habitats for multiple species (Mitchell et al., 2019; Ranius et al., 2009).

In Sweden, the abundance of oak has substantially declined, today representing only 20-35% of historical maximum. This reduction was caused by a long-term decline in oak forests, with the most significant decrease in 18th and 19th centuries (Lindbladh & Foster, 2010). In Southern Sweden the decline in general was driven by the expansion of agriculture, while in other regions it was associated with changes in forest management and promoting faster-growing Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). Despite historical decline oak may benefit from ongoing climate change (Vitasse et al., 2019). Model predictions indicate northward expansion of oak distribution in Sweden under future climate scenarios (Dyderski et al., 2025).

Climatic drivers of oak growth

Oak growth is influenced by many environmental factors, particularly by climatic conditions. Water availability and temperature have been identified as the main factors that affect radial growth (Árvai et al., 2018; Drobyshev et al., 2008; Netsvetov et al., 2017). Water availability during growing season, especially low precipitation during spring and early summer reduces the annual tree ring widths (Basu et al., 2024; Drobyshev et al., 2008; Vitasse et al., 2019). Late summer droughts may cause negative effects on growth not only in the current but also in the next growing season (Drobyshev et al., 2008; Netsvetov et al., 2017).

Temperature effects on oak growth depend on season. High temperatures in summers may affect the growth by increasing drought stress (Árvai et al., 2018; Drobyshev et al., 2008). Higher temperatures in the autumn can lead to increase in growth, which can be linked to longer physiological activity and efficient carbohydrate translocation and storage, which increase early wood formation in the next spring (Drobyshev et al., 2008). Temperature during winter and early spring also influences growth. Extremely low temperatures can lead to significant growth reductions (Helama et al., 2009; Scharnweber et al., 2013). In particular

late frosts have been observed to damage tissues and affect cambial activity (Drobyshev et al., 2008).

Drought causes significant declines in oak growth. These growth reductions are usually driven by physiological responses to water deficiency in the soil. In response to drought stomatal conductance and leaf transpiration decline and cause decline in net photosynthesis (Niemczyk et al., 2025; Rolando et al., 2025). Carbon assimilation becomes limited, because trees prioritize survival and maintenance processes over carbon allocation to growth during drought events (Rolando et al., 2025).

Oak exhibits several mechanisms to buffer drought effects. The species is characterized by relatively high intrinsic water-use efficiency and tight stomatal regulations (Nosenko et al., 2025). During droughts oak leaves have higher density of stomata with reduced area, which helps to adapt gas exchange to water deficiency (Niemczyk et al., 2025). Osmotic adjustments allow oak to maintain cell turgor at lower water potentials, resulting in continued stomatal conductance and gas exchange and thus delaying growth reduction (Čater, 2011).

Radial growth at breast height

Tree ring widths measured at breast height are often used as a proxy for growth responses to environmental factors. Most studies investigating oak responses to climate rely on increment cores collected at breast height to assess growth sensitivity to climate variability (Helama et al., 2014; Litovchenko et al., 2024; Skiadaresis et al., 2019). The measurements are limited to only a single point along the stem and thus this approach does not account for potential variation in the tree growth at different heights.

Evidence from other species indicate that growth dynamics and responses to drought may vary along the stem. Trees exhibit certain growth patterns along the stem, often prioritizing upper sections during early stages of growing season. Later the growth allocation shifts towards breast height, which can be also altered by drought conditions (Schäfer et al., 2019). Similar patterns were observed in *Populus euphratica*, where radial growth responses showed high variability along the stem sections (Abdureyim et al., 2023).

Many studies have demonstrated that drought negatively affects radial growth based on increment cores sampled at breast height. These studies do not quantify empirically reconstructed volume increments and assess growth at one height. It results in limited information on vertical distribution of growth responses along the stem. Growth responses are usually assessed for selected drought years and not for a continuous gradient of drought severity.

Stem analysis provides detailed information on radial growth at multiple heights and allows precise reconstruction of annual tree volume increment. This approach captures variation in height growth and integrates measurements of diameter growth at different tree heights. However, stem analysis is highly invasive and requires felling trees, which limits its applicability. In contrast, increment cores collected at breast height are less invasive, more cost effective and efficient to process.

In this study I use stem analysis technique to reconstruct annual volume increment and assess growth responses of oak to drought along the stem. I identify a drought intensity at which oak growth starts to decline by combining annual volume increments to a broad gradient of drought intensity. I also estimate the length of the growth decline when such occurred. Specifically, I decided to test following hypotheses:

H1: Oak radial growth is primarily limited by drought rather than temperature alone.

H2: Drought-induced growth responses vary along the stem.

H3: Severe drought conditions result in prolonged growth recovery periods.

H4: Oak volume increment declines only under severe droughts.

2. Material and methods

Study area

I sampled four sites within the Tönnersjöheden experimental forests, Halmstad municipality, and one site - in the Skarhult experimental forest, Eslöv municipality (Figure 1). The average annual temperature in the northern section of the study area is 8.4 ℃ with the annual precipitation being 849.9 mm. For the southernmost site, the average temperature is 9 ℃ and the annual precipitation is 676.0 mm (SMHI, 2021). The sites differed in soil moisture, ranging from fresh-dry to moist-fresh soils (Table 1).

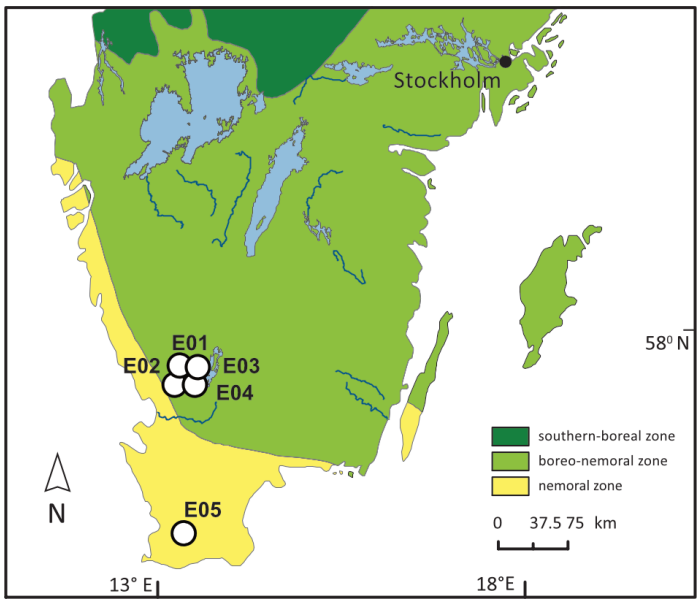

Figure 1. Location of study sites.

Field sampling

I conducted the sampling in even-aged oak stands typical for the study area. Sites were selected to be at least 60 years old to ensure that tree growth chronologies included multiple droughts, allowing the assessment of growth responses to a gradient of drought conditions. At the same time, I tried to choose sites with different soil conditions and past management practices.

Within each stand, I selected trees based on their size, social position, and vitality. Selected trees were representative, meaning that they belonged to the main canopy layer and exhibited dimensions typical for the stand. Trees showed well-developed crowns and no visible damage such as double tops or scars on the main stem that could be indicative of the past disturbances, which could dilute climate-

growth relationship. In Skarhult, I selected trees from those marked to be removed in a planned thinning.

Selected trees were felled and I then measured tree's total height and crown height. Discs were collected from every two meters along the stem, including at the base and breast height, continuing until the stem diameter was less than five centimeters. In total, 263 discs were collected from 26 trees. The labor-intensive nature of stem analysis method and constrains imposed by sampling permissions limited the number of trees sampled within a site by five. To partially compensate for limited number of trees, I invested in collecting between 9 and 13 cross sections per sampled tree (tree characteristics Appendix 1, Table A1).

Table 1. Site characteristics of studies oak stands. Treatments refer as a year of partial thinning. Soil moisture estimation was obtained from the SLU soil moisture map (SLU, 2025) and represents soil moisture based on topography, climate and soil type. Est. refers to year of establishment and BA to stand basal area. Parentheses indicate values including understory.

SiteID	Treatments	Est.	Soil	BA (m^2/ha)	Density (st/ha)
E01	1961, 1966, 1976, 1981, 1986, 1995, 2000, 2016	1926	fresh-dry	16.5 (21.2)	220 (883)
E02	1973, 1983, 1996, 2018	1930	fresh-dry	22.1	416
E03	1985, 2009	1945	fresh-dry	18.0	756
E04	NA	NA	fresh-dry	18.2	452
E05	1991, 1996, 2004, 2010, 2016	1950	moist-fresh	18.4	296

Sample processing

I cut samples into rectangular pieces to speed up their drying and facilitate their polishing and scanning. The samples were dried at room temperature for approximately four weeks. After drying, samples were polished using gradually finer grits of sandpaper (40, 80, 120, 240, 320). Finally, the samples were scanned at 2400 DPI resolution. Tree ring widths were measured on the scanned samples using Cybis CooRecorder 9.8.1 software (Cybis Elektronik & Data AB, 2022). All tree ring chronologies were dated using regional oak chronologies (Drobyshev et al., 2008) and verified by the point-year method.

Data analysis

For each tree, I averaged two radii originating from one sample to obtain the mean growth chronology for a given height and for a given tree. No detrending was applied to the data at this stage since the goal of the analysis was to track growth

responses to drought on the non-normalized data, preserving the original scale of measurements.

I reconstructed annual volume increments using stem analysis technique. This method integrated growth information from samples collected at different height of the main stem, accounted for differences in growth dynamics along the tree stem and variation in tree height growth. For each section of the stem, I calculated volume using formula for a truncated cone,

$$V = \frac{\pi L}{3}(r_1^2 + r_1 r_2 + r_2^2)$$

where r_1 and r_2 are radii at lower and upper ends of the section and L is lengths of the section. I summed all of the section volumes to obtain whole stem volume and then I calculated annual volume increments as a difference between volumes in two consecutive years. The output of stem analysis was annual volume increment chronology for each individual tree. For the purposes of subsequent analyses, volume increment reconstruction obtained by stem analysis technique was regarded as correct representation of growth dynamics ("ground truth").

Response function analysis of climate-growth relationship

Climate data used in subsequent analysis consisted of monthly temperature and precipitation from European Reanalysis dataset ERA5 (Hersbach et al., 2020), obtained for each of the study sites. Climate data was used to calculate potential evapotranspiration (PET), with Penman-Monteith method (Howell & Evett, 2004) and Standardized Precipitation Evapotranspiration Index (SPEI). SPEI reflected a monthly water balance between precipitation and PET. SPEI is standardized relative to a reference period, which allowed to compare sites with different climatic conditions. It was calculated at several temporal scales (from one to several months) to test for sensitivity of growth dynamics to a particular SPEI formulation and used in subsequent analyses.

To test H1, I used response function analysis (Zang & Biondi, 2015) to quantify how monthly climate variability influenced oak radial growth at breast heigh. This method allowed estimating unique contribution of individual climatic variables to tree growth, even when the predictors were correlated with each other.

Climatic predictors were transformed into independent components and then related to the tree ring chronology. As a result, this method reduced the influence of autocorrelation and collinearity among climate variables. The analysis operated at monthly resolution, allowing to identify periods of the year during which climate conditions had the strongest influence on growth. Statistical significance of response function coefficients was assessed by bootstrapping.

As growth input, I used tree ring chronologies obtained from cross section cut at the breast height (dbh). Single tree chronologies were detrended using a spline with the 50% frequency cutoff at 32 years to preserve annual and decadal variability in growth while removing age-related artifacts in the chronology. Site chronologies were constructed by aggregating detrended tree level indices using a robust biweight mean, with prewhitening applied to reduce auto correlation.

Standardized Precipitation Evapotranspiration Index (SPEI) and temperature at 2 m (t2m) were used as climatic predictors. I regarded SPEI as a drought proxy since it accounted for both precipitation and atmospheric evaporative demand and provided assessment of drought intensity and timing under varying temperature conditions. Preliminary analyses indicated that SPEI calculated at the three-month scale had the most statistically significant relationship with oak growth. I therefore selected SPEI3 for the response function analysis.

Identification of site-specific drought years

Extreme drought events were identified for further analysis separately for each site based on SPEI values. Relying on the results of response function analysis (see the section above), I identified SPEI3 as the best drought proxy. For each site, I selected years with the lowest SPEI3 in June. For Tönnersjöheden sites (E01-E04) I selected the same set of drought years. The decision was justified by their close spatial proximity, which resulted in highly synchronized SPEI3 values and identical timing of droughts.

I applied two different selection protocols, depending on the analysis. First, to assess duration of growth recovery after severe droughts, I selected three years (Rank 1-3) with the lowest SPEI3 values. These years represented the most extreme drought conditions and were used in subsequent recovery analysis. Second, to conduct the threshold analysis, I selected ten driest years (Rank 1-10), realizing that not all of them were actually drought years. This relaxed version of selection protocol, however, allowed me to extend the gradient of drought conditions towards non-extreme situations and comfortably capture the drought level associated with growth decline.

Analysis of growth response to drought

I assessed growth response to drought using two alternative approaches. First, observed growth was divided by the growth projected under the assumption of no drought. Values below 1 indicated a negative response, while the values above one suggested that the tree improved the growth following the drought. Second, projected growth was subtracted from observed growth to assess the response while maintaining the absolute scale of measurements. In this case, negative delta

values indicated drought-induced growth reduction and positive values – a positive response to drought.

Both protocols relied on projected growth, which was estimated on volume increment reconstructions, using flexible (*df* = 5) polynomial spline fit to the section of the volume growth chronology, preceding the event year (i.e. the drought year). The spline generated growth projection for the years following the drought year, under the assumption that growth was driven exclusively by the age-vs.-growth relationship and recent decadal scale growth dynamics. I estimated projected growth independently for each tree (in total 26 trees), using stem analysis annual volume chronologies for each identified drought year (10 drought years), which resulted in 260 projections.

Vertical distribution of drought responses

To test H2, I analysed the vertical distribution of growth response along the stem to selected droughts. Each stratum was represented by tree ring widths from a disc collected at a specific height along the stem (0, 2, 4, 6, 8 m). To address variability of increments in higher crown strata, heights from 9 m and above were aggregated into a single chronology. Growth responses to drought were assessed by dividing observed tree ring widths by projected. Projected growth was obtained the same way as in the previous section, but instead of volume increment I used tree ring widths collected at different heights along the stem. The aim of the analysis was to test whether drought induced growth responses were consistent along the stem or differed on different heights.

Growth recovery after drought

To test H3, growth recovery was defined as the year (later referred to as *recovery year*), when the observed growth reached 95% or above of the projected growth. The duration of recovery period was defined as the period between the drought year and the recovery year. I studied the growth recovery pattern only for most severe drought events (see subsection *Identification of site-specific drought years*). This ensured that growth recovery dynamics were assessed following clearly defined and biologically meaningful droughts. I evaluated growth recovery for each tree, separately for each drought event, which resulted in a total of 78 tree-event combinations.

Threshold analysis

To test H4, I conducted threshold analysis to identify the level of drought severity at which oak volume growth response shifted from neutral or positive to negative. Drought severity was quantified using SPEI3, and growth response metrics were derived as in the previous section (*Analysis of growth response to drought*).

To estimate drought thresholds, growth responses were related to SPEI3 using polynomial regression fitted to all individual tree responses to each analyzed drought across sites. I identified two threshold SPEI values. The first threshold was defined as the SPEI value at which the fitted mean response crossed the neutral response line (1 for ratio-based response and 0 for the absolute response). The second threshold was defined as the SPEI value at which the upper 95% confidence limit crossed that line, indicating statistically significant response.

Tree resilience components

I calculated Lloret's components of tree resilience: resistance (Rt), resilience (Rs) and recovery (Rc) (Lloret et al., 2011), as a complementary analysis to compare projection-based growth response estimates with a standard approach commonly used in dendroecology. Because tree growth generally increases with age and size, and these indices reflect pre drought growth levels, they may not fully account for long term growth patterns. I decided to use them to verify whether both methods give similar conclusions and whether results of this study may be comparable with other studies.

The indices were calculated for drought years identified in the section *Identification of site-specific drought years*, which I divided into three drought severity classes based on SPEI values: extreme (<-2.0), severe (between -2.0 and -1.5) and moderate droughts (between -1.5 and -1.0). I calculated the indices from breast height tree ring chronologies converted to basal area increment (BAI). Basal area was reconstructed from a sum of ring widths, and BAI was calculated as a difference in BA between consecutive years. Resistance was calculated as a ratio of growth during the drought to growth from before drought, recovery as a ratio of growth after the drought to growth during the drought and resilience as a ratio of growth after the drought to the growth from before the drought. Growth before drought and after drought represented mean value of growth during three years respectively preceding or following the drought event.

For testing the statistical significance of drought severity on resilience components, I developed linear mixed effects models. I used one of the resilience components (Rt, Rs or Rc) as a response variable, drought severity class as a fixed effect, tree and site as random effects. The significance was tested using ANOVA.

Data processing and workflow

I prepared the datasets for subsequent analyses. I processed tree ring measurements and reconstructed total stem volume and volume increments using stem analysis. I also calculated tree resilience components myself. Response function analysis, recovery duration analysis and threshold analysis followed the protocol developed by Igor Drobyshev (unpublished R scripts). I ran the analysis, adapted to my dataset, prepared figures and summaries presented in the thesis.

I conducted all of the analyses in R version 4.5.2 (R Core Team, 2025). I processed tree ring data using *dplR* package (Bunn, 2008). For climate data and drought quantification I used *terra* (Hijmans, 2025), *SPEI* (Beguería & Vicente-Serrano, 2023) and *treeclim* (Zang & Biondi, 2015). For modeling I used *lme4* (Bates et al., 2015) and *lmerTest* (Kuznetsova et al., 2017). For handling the data and final visualizations I used *dplyr* (Wickham et al., 2023), *tidyr* (Wickham et al., 2025), *ggplot2* (Wickham, 2016) and *patchwork* (Pedersen, 2025).

3. Results

General growth characteristics of analyzed trees

I analyzed 26 trees from five sites with five trees per site, except site E02 where I sampled six trees. The age of the trees ranged from 66 (tree E0502) to 192 years (tree E0421) with a mean age of 98.8 ± 29.1 years. Tree height ranged from 16.3 m to 24.3 m with mean height of 20.0 ± 2.3 m.

Annual volume increment strongly differed among trees and sites. Mean annual volume increment ranged from 0.00212 ± 0.00241 m^3 per tree (E0421) to 0.01820 ± 0.01390 m^3 per tree (E0502) (Figure 2). Site E05 showed the highest mean annual volume increment (0.01411 ± 0.01093 m^3), while sites E01, E02, E03 and E04 showed significantly lower mean increments, ranging from 0.00392 to 0.00667 m^3 per year.

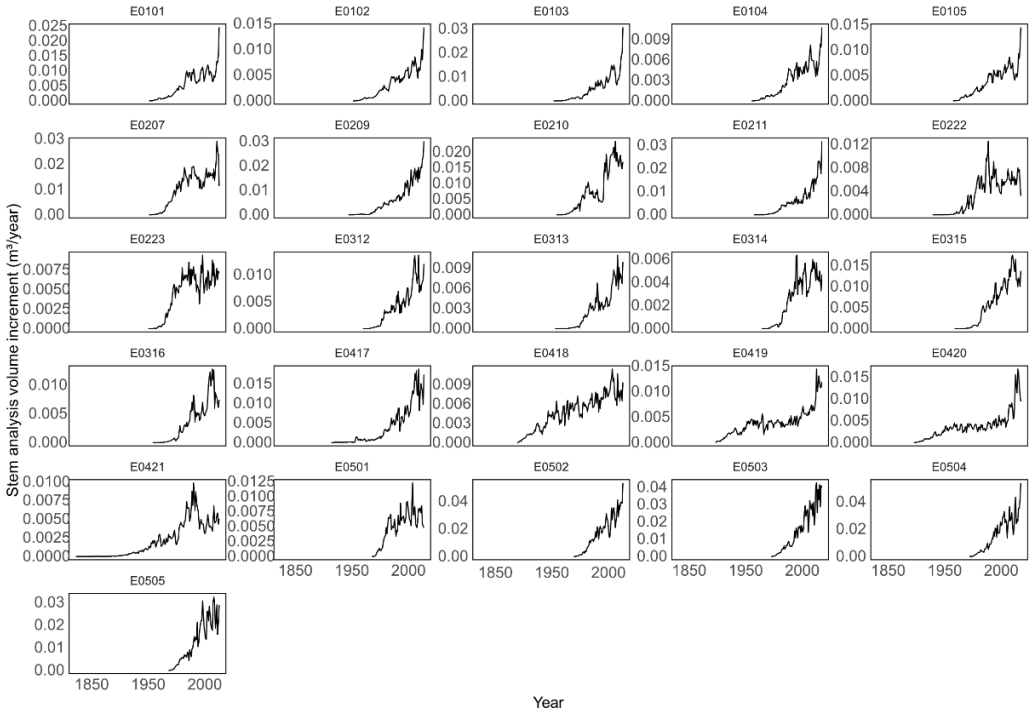

Figure 2. Annual volume increment (m^3) of individual trees across all sites, obtained from stem analysis.

Climate-growth relationship

Spring and early summer drought influenced tree ring widths at breast height, while temperature effects were weaker and less inconsistent. SPEI showed a significant positive relationship with tree ring widths at three sites, but with differing timing. At site E01 tree ring widths showed significant response to SPEI in March, May and June. At site E02, the response function coefficient was significant only in June. At site E03, significant relationship occurred in May and June. Sites E04 and E05 showed no significant response of tree ring widths to SPEI. Air temperature showed weaker relationship with growth. A statistically significant response of tree ring widths to temperature was observed only in June and August at site E02, while no significant effects occurred at other sites (Figure 3, Table 2, Appendix 2, Table A2).

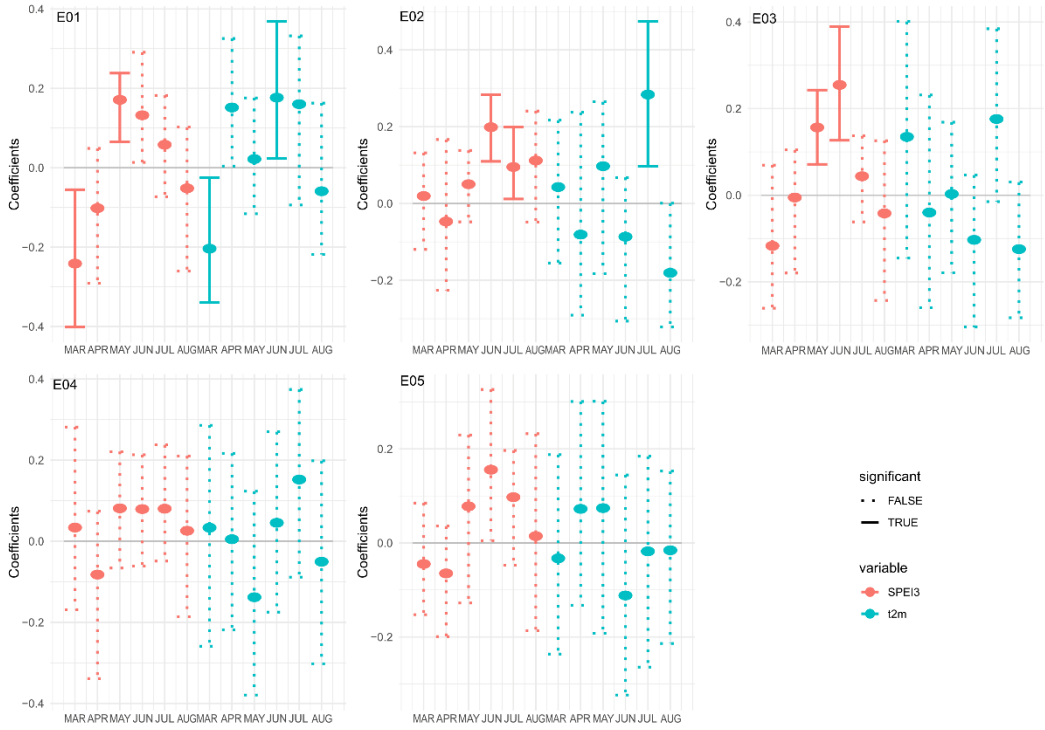

Figure 3. Relationship between climatic variables and tree ring width indices, as revealed by response function analysis. Red lines represent SPEI (Standardized Precipitation Evapotranspiration Index), while blue lines represent correlations with temperature at 2 m (t2m). Solid lines indicate statistically significant relationships and dashed lines indicate non-significant relationships.

Table 2. Summary of response function coefficients. For each variable (SPEI3 and temperature at 2 m) and month (from March to August), the table shows median, the range of coefficients and number of sites with significant coefficients across sites (Number_sig).

Variable	Month	Median	Minimum	Maximum	Number_sig
SPEI3	March	-0.0409	-0.2400	0.0318	1
	April	-0.0679	-0.1032	-0.0122	0
	May	0.0780	0.0488	0.1704	2
	June	**0.1557**	**0.0834**	**0.2530**	**2**
	July	0.0841	0.0505	0.0972	1
	August	0.0132	-0.0507	0.1156	0
t2m	March	0.0339	-0.1976	0.1234	1
	Aril	-0.0065	-0.0858	0.1517	0
	May	0.0235	-0.1425	0.0986	0
	June	-0.0892	-0.1115	0.1766	1
	July	0.1595	-0.0179	0.2925	1
	August	-0.0592	-0.1875	-0.0163	0

Drought thresholds and site-specific sensitivity

Drought intensity controlled volume growth response across all sites. I identified SPEI value below which observed volume increment dropped below projected volume increment values, based on growth responses to 10 droughts (Appendix 3, Table A3). Across all sites, growth declined when SPEI dropped below -1.87, with mean volume loss of 0.0182 ± 0.0401 m^3. However, the departure from the mean growth was statistically significant below SPEI of -2.14 with mean volume loss below this value of` 0.0193 ± 0.0419 m^3 (Figure 4). For the ratio-based response (observed / projected volume increment) the SPEI3 thresholds were respectively -1.48 and 1.94 (Figure 5).

Sites showed significant differences in the drought sensitivity. The most sensitive site was E03 with a threshold SPEI value of -1.06, followed by site E04 (-1.12), E02 (-1.36) and E01 (-1.74). The least sensitive was site E05, where only the most severe drought conditions with threshold SPEI value of -2,06 resulted with negative growth response.

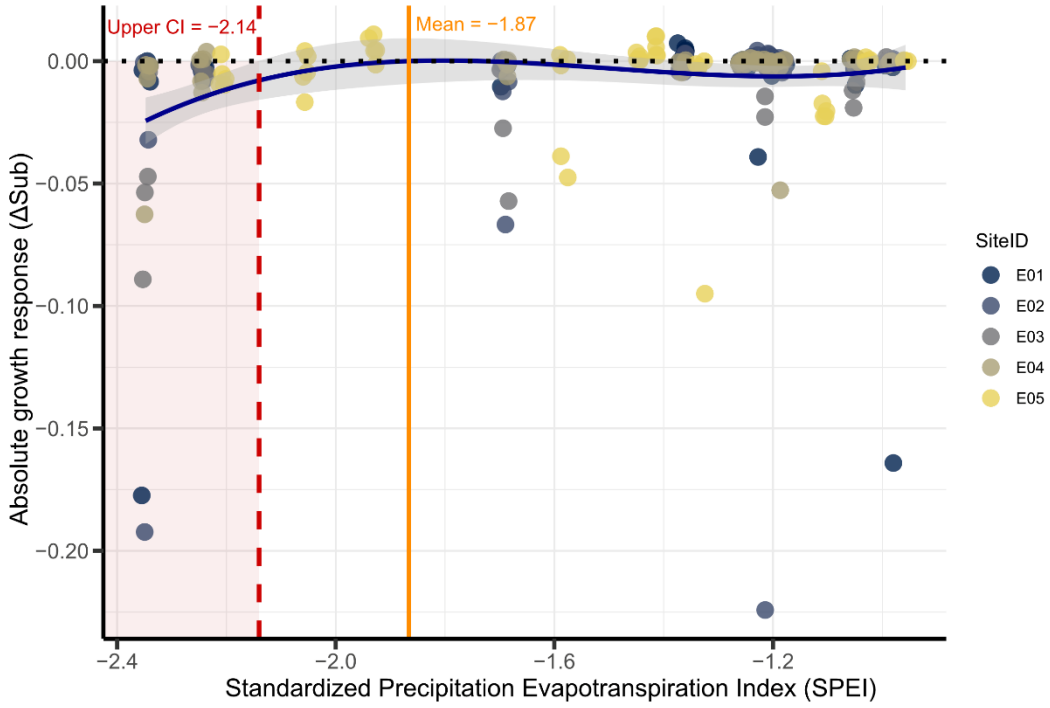

Figure 4. Relationship between climatic conditions (SPEI) and absolute growth response (Δsub = observed - projected volume increment) combined for all sites. Each point represents an individual tree response under specific climatic conditions. The orange line indicates the threshold for all sites combined, below which growth response became negative. The red dashed line indicates the SPEI threshold below which growth showed statistically significant negative departure.

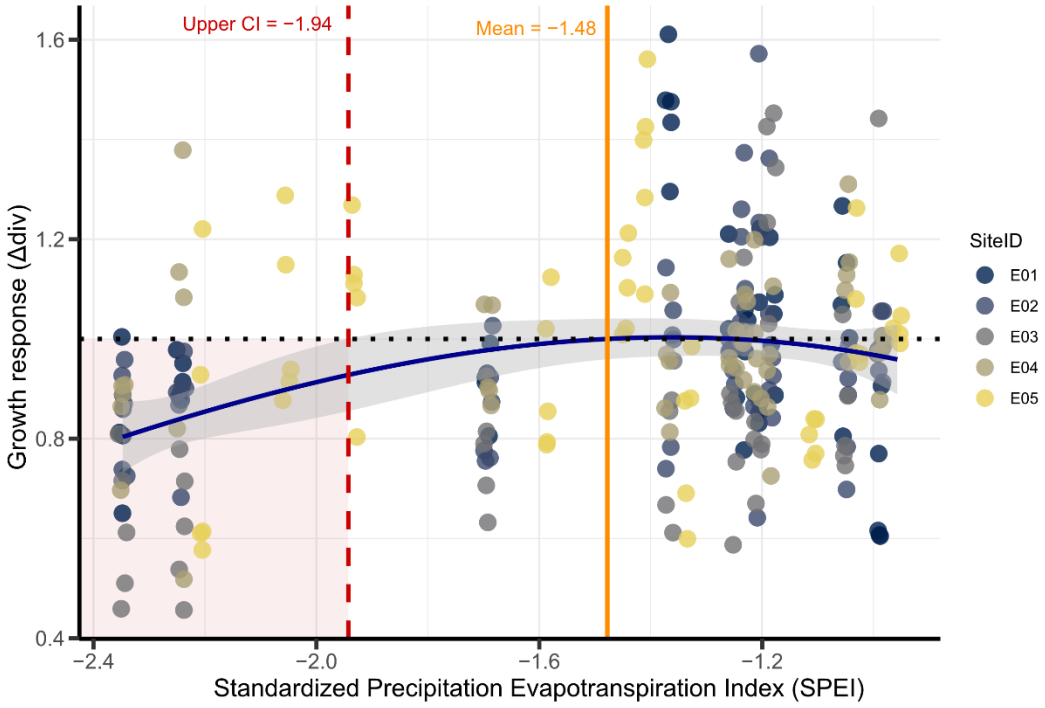

Figure 5. Relationship between climatic conditions (SPEI) and growth response (Δdiv = observed/projected volume increment) combined for all trees. Each point represents an individual tree response under specific climatic conditions. The orange line indicates the threshold for all sites combined, below which growth response became negative. The red dashed line indicates the SPEI threshold below which growth showed statistically significant negative departure.

Tree growth recovery following severe droughts

Based on tree growth responses to three most severe droughts, in 57.7% of the cases, there was no growth decline observed. For the trees which faced the growth decline, 12.8% needed more than 10 years to recover. In 10.3% of the cases the trees recovered within 3 years. Recovery period of 2 years occurred in 7.7% of cases, 4 years in 5.1% of cases and 7 years in 2.6% of cases (Figure 6).

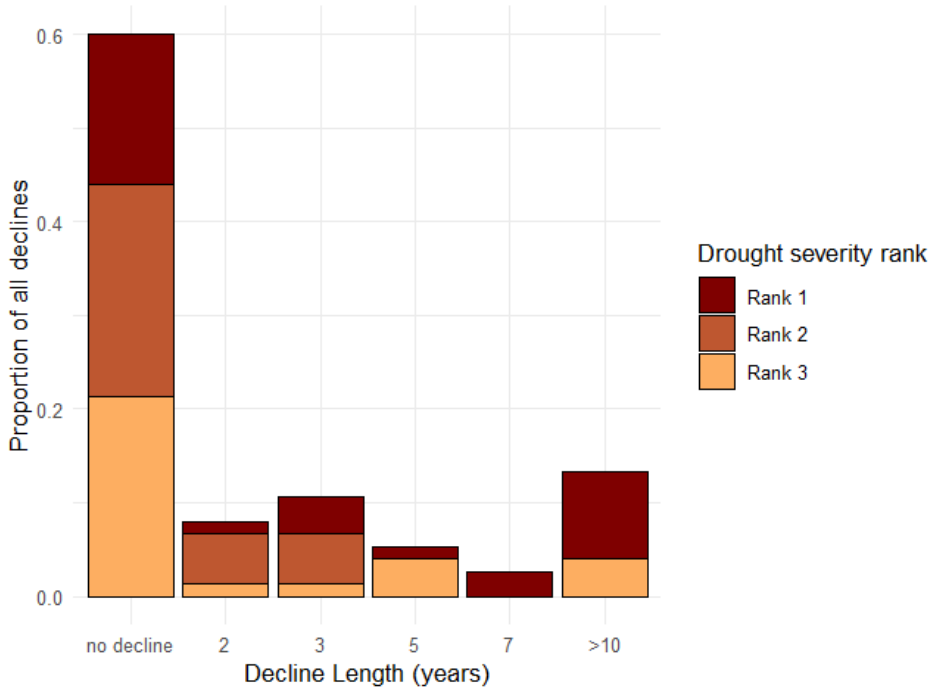

Figure 6. Duration of growth decline following three most extreme drought events for all 26 trees.

Tree resilience components

Resistance decreased with increasing drought severity, mean resistance for extreme droughts (SPEI < -2.0) was 0.79 ± 0.21, while for severe (-2.0 to -1.5) and moderate (-1.5 to -1.0) droughts it was respectively 0.95 ± 0.22 and 1.01 ± 0.26. For recovery the pattern was weaker, with values of 1.26 ± 0.26 for extreme droughts and 1.09 ± 0.26 for severe droughts. Trees showed relatively high resilience to drought with values close to 1 (0.98 ± 0.28, 1.01 ± 0.19 and 1.20 ± 0.51), indicating that although growth dropped during the drought it returned to pre droughts levels (Figure 7). Drought severity had a significant effect on tree resistance ($p < 0.001$), while effects on recovery ($p < 0.05$) and resilience ($p < 0.01$) were less significant, however, the variability between trees and sites was large (Appendix 4, Figures A1, A2, A3).

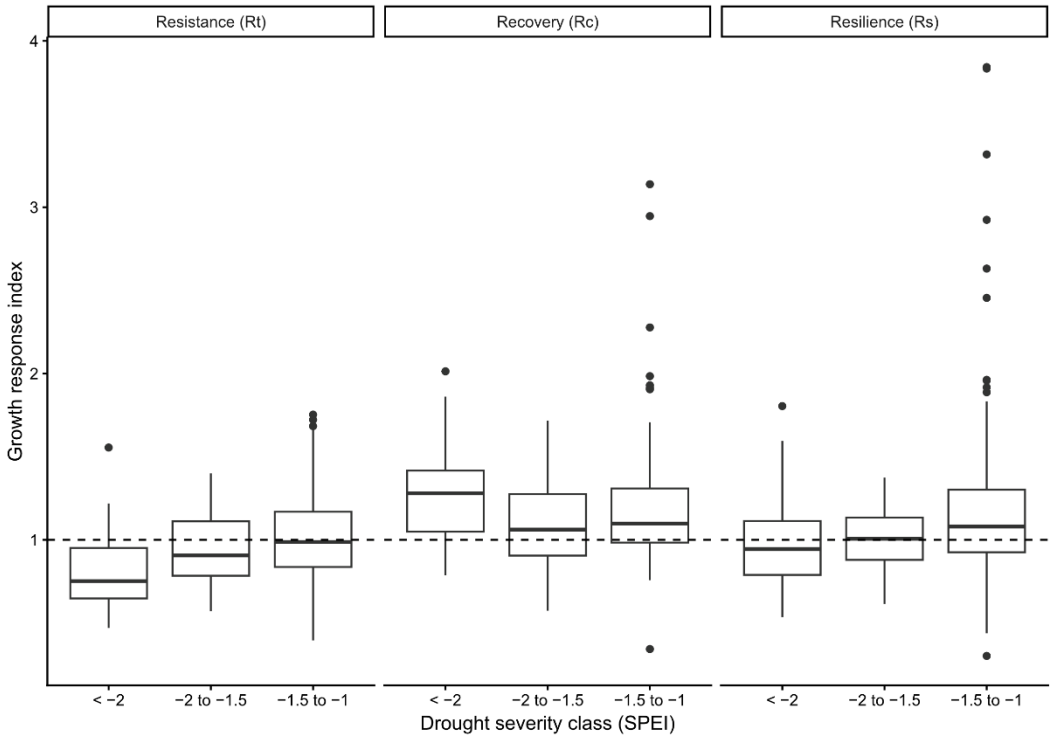

Figure 7. Tree resilience components (resistance, recovery and resilience) across drought severity classes. Indices are grouped by drought severity based on SPEI3 values (< -2.0 extreme, -2.0 to – 1.5 severe, -1.5 to -1.0 moderate). The boxes show distribution of indices calculated from basal area increment at breast height (in total 26 trees, 5 or 6 per site). The dashed horizontal line indicates 1, which means no growth reduction relative to pre drought growth rates (Rt = 1), no return to pre drought growth (Rc = 1) and return to pre drought growth (Rs = 1).

4. Discussion

In this study I examined the relationship between oak volume growth and climatic conditions, with a particular focus on extreme drought events. Drought intensity, rather than temperature alone, controlled oak growth. Contrary to expectations, growth responses to drought were consistent along the stem, showing no differences at varying heights.

Climate-growth relationship of oak

Response function analysis revealed that oak volume growth was significantly related to SPEI3 during spring and early summer, identifying this period as crucial for drought sensitivity. It suggests that water availability during this period has a strong influence on volume increment, which is consistent with previous studies showing that SPEI3 (Roibu et al., 2020) or precipitation in spring and early summer are crucial for oak growth in several regions in Europe (Bose et al., 2021; Drobyshev et al., 2008; van der Werf et al., 2007). Trees are particularly sensitive to drought during this period due to high cambial activity and intensive wood formation. Physiologically, drought induces stomatal closure and increased oxidative stress, which reduce carbon assimilation and lead growth losses (Stojnić et al., 2016).

In contrast, response function coefficients for air temperature were weaker and less significant. Similar results have been reported in other studies, where temperature did not show as strong effects as water availability (Bose et al., 2021; Drobyshev et al., 2008; Kuster et al., 2013). Pedunculate oak occupies a broad ecological range of sites across Europe, including areas with relatively high mean temperatures (Díaz-Maroto et al., 2007). As a result of high plasticity, temperature effects are usually indirect and can be mitigated by sufficient water availability. This explains why SPEI, which integrates both precipitation and evaporative demand was a better predictor of volume losses than temperature alone.

Thresholds behavior and growth response to drought

Oak exhibited high resistance to drought. The threshold analysis revealed significant growth reduction under SPEI of -2.14 and considering that SPEI between -1.5 and -1.0 indicates moderate drought, -2.0 and -1.5 severe drought and ≤ -2 extreme drought (Mckee et al., 1993; Wang et al., 2014), in my study growth declined only under extreme water deficit, while it remained similar under moderate and severe droughts. This pattern is consistent with previous findings describing oak as a drought tolerant species (Epron & Dreyer, 1993). The resistance is likely related to morphological and physiological plasticity and

mechanisms, such as high intrinsic water-use efficiency (Nosenko et al., 2025), increasing stomata density with reduced area (Niemczyk et al., 2025) or osmotic adjustments (Čater, 2011), which allow oak to buffer the negative effects of water deficit and maintain growth. However, under prolonged or consecutive droughts these buffering mechanisms may become insufficient, leading to growth reductions (Stojnić et al., 2016).

Negative growth response to drought thresholds were site-specific, suggesting that site conditions influence oak sensitivity to drought (Appendix 5, Figure A4). Site E05 exhibited the lowest sensitivity to drought with lowest SPEI3 threshold, which may be explained by higher soil humidity and relatively large number of thinnings (5) compared to other sites. The most drought sensitive site (E03) has been thinned only twice, while less sensitive sites E01, E02 and E05, respectively 8, 4 and 5 times. The results align with previous studies, showing that relationship between climate and growth depends on local site-specific environmental factors (Bose et al., 2021), and frequent thinnings, which may increase tree resistance (Barbeito et al., 2024). Thinnings reduce competition by reducing number of trees, which increases the amount of available water and resources. Tree age is known to influence the drought resistance. Previous study showed that older trees usually show better resistance to climatic variability (Skiadaresis et al., 2019), which may be explained by more developed root systems and higher storage capacity (Arain et al., 2022). However, in my study the differences could not be confirmed due to small age differences.

Recovery dynamics

Most of the trees in the study showed either no response to drought or relatively fast recovery after drought, with observed growth reaching projected within the same year. Similar recovery patterns have been reported for young oaks, where tree growth rapidly recovered after water stress (Kuster et al., 2013). Fast recovery may depend on the timing of drought. Earlier study showed that growth recovery after spring droughts was longer compared to summer droughts (Bose et al 2021). Spring is a period of high cambial activity and water deficiency during that time may lead to more significant growth reductions.

Tree resilience indices supported the recovery analysis. Trees showed a significant decline in resistance (Rt) only under extreme droughts, while recovery (Rc) and resilience (Rs) remained more stable. It indicates that oak returned to growth rates from before drought within a short period of time. Similar patterns were observed in other study, were trees showed a decline in growth during drought but relatively fast recovery and high resilience (Barbeito et al., 2024).

Individual trees exhibited varying drought responses and recovery even within the same sites. The variability may be related to root system depth and access to deeper water reserves. Previous research showed that trees exhibiting stronger growth declines had shallower root systems compared to drought resistant individuals (Ripullone et al., 2020). Oak typically forms a deep taproot, but root structure may significantly vary between trees even within one stand (Mauer et al., 2017) and form of root system may influence growth responses to drought (Kościelniak-Wawro et al., 2025).

Growth response to drought along tree stem

Growth responses were consistent at different stem heights. Contrary to initial hypothesis, I found no vertical differences in drought response along the stem. Previous studies indicated changes in tree growth patterns along the stem under drought conditions (Abdureyim et al., 2023; Schäfer et al., 2019), which suggested different growth responses at different heights. In my study I found that drought effects on volume increment were uniform in the whole tree.

Study limitations and future research

I based this study on data from five sites located in two areas in southern Sweden, which represent a relatively narrow gradient of climatic and site conditions. In particular, I did not include any sites from eastern part of southern Sweden. That region is often characterized by generally drier conditions. Including a broader climatic gradient in future studies would probably allow to assess the drought effects in more contrasting conditions.

I limited the number of sampled trees because of labor-intensive, destructive sampling and extensive sample preparation. I preferred more detailed vertical reconstructions for fewer trees instead of larger number of trees with fewer samples taking along the stem. However, this approach provided limited information of growth response at the stand-level. Future studies should combine sampling at different heights with larger datasets obtained by using non-destructive methods.

5. Conclusions

- Oak growth was negatively affected mainly by severe and extreme droughts, indicating that this species shows relatively high resistance to water stress.
- Drought sensitivity was site-specific, with trees growing on more humid sites showing growth decline only under most extreme droughts.
- Oak recovery from drought-related growth decline differed between trees, ranging from two years to more than 10 years.
- Many trees did not exhibit significant growth decline even under severe drought conditions, highlighting the drought resistance of oak.

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Popular science summary

Changing climate causes periods with when trees have not enough water to become more frequent and intense. This affects tree growth and the functioning of forest ecosystems. Pedunculate oak is a very important species in Sweden because of its ecological values and wood with high quality. Today oak is not the most common species, but projections suggest that oak may expand its geographical range further to the north in the future.

In this study, I assessed how oak trees respond to droughts in terms of volume growth. I focused on effects of temperature and water availability on growth and recovery after drought and sensitivity of oak to water shortage. Water availability was the most important factor influencing the growth of oaks. Droughts in spring and early summer caused growth reductions, at the same time temperature alone had no visible effect. Growth responses differed among sites and individual trees, but most trees recovered their growth within one year after the drought. Growth reduction was similar at different heights along the tree stem, indicating that drought effect was even in the whole tree.

Appendix 1. Tree characteristics

Table A1. Tree diameter at breast height, height, age estimated from disc collected at tree base, total stem volume calculated using stem analysis.

TreeID	Dbh (cm)	Height (m)	Age (years)	Vol_stA (m3)
E0101	26.4	19.5	94	0.517
E0102	21.6	18.5	95	0.316
E0103	25.7	20.1	93	0.472
E0104	19.3	16.3	94	0.275
E0105	22.2	18.2	91	0.336
E0207	32.7	24.3	94	0.967
E0209	27.6	22.3	101	0.630
E0210	27.3	20.7	89	0.668
E0211	24.5	22.2	91	0.527
E0222	23.7	17.9	118	0.404
E0223	21.0	20.4	95	0.417
E0312	23.6	19.3	82	0.337
E0313	18.9	18.9	91	0.256
E0314	17.6	17.9	81	0.206
E0315	27.2	20.1	89	0.513
E0316	20.4	18.2	89	0.324
E0417	25.7	18.7	124	0.486
E0418	31.7	18.6	141	0.670
E0419	29.4	16.7	142	0.568
E0420	27.6	18.8	143	0.546
E0421	23.8	17.9	192	0.387
E0501	21.3	21.6	70	0.346
E0502	36.5	23.7	66	1.127
E0503	34.6	22.7	68	1.032
E0504	36.5	23.4	69	1.113
E0505	32.3	24.2	68	0.864

Appendix 2. Response function summary

Table A2. Response function coefficients for each month across sites.

Site	Variable	Month	Coefficient	Significance
E01	SPEI3	March	-0.240012111	*
	SPEI3	April	-0.103239789	
	SPEI3	May	0.170438679	*
	SPEI3	June	0.133064622	
	SPEI3	July	0.057953719	
	SPEI3	August	-0.050730659	
	t2m	March	-0.197643511	*
	t2m	Aril	0.151733016	
	t2m	May	0.023503283	
	t2m	June	0.176852854	*
	t2m	July	0.159467461	
	t2m	August	-0.059199579	
E02	SPEI3	March	0.026185298	
	SPEI3	April	-0.048348754	
	SPEI3	May	0.048796773	
	SPEI3	June	0.200033394	*
	SPEI3	July	0.096574241	*
	SPEI3	August	0.115550807	
	t2m	March	0.040088382	
	t2m	Aril	-0.085788758	
	t2m	May	0.098598587	
	t2m	June	-0.089237988	
	t2m	July	0.292496061	*
	t2m	August	-0.187465854	
E03	SPEI3	March	-0.113531749	
	SPEI3	April	-0.012165517	
	SPEI3	May	0.155535837	*
	SPEI3	June	0.252993238	*
	SPEI3	July	0.050500727	
	SPEI3	August	-0.030728739	
	t2m	March	0.123444798	
	t2m	Aril	-0.039929396	
	t2m	May	0.005420042	
	t2m	June	-0.095473072	
	t2m	July	0.180014807	
	t2m	August	-0.125719313	

Site	Variable	Month	Coefficient	Significance
E04	SPEI3	March	0.031837039	
	SPEI3	April	-0.082341816	
	SPEI3	May	0.077981830	
	SPEI3	June	0.083424310	
	SPEI3	July	0.084115667	
	SPEI3	August	0.034834520	
	t2m	March	0.033912032	
	t2m	Aril	-0.006495670	
	t2m	May	-0.142524473	
	t2m	June	0.050681437	
	t2m	July	0.153903590	
	t2m	August	-0.054214292	
E05	SPEI3	March	-0.040867371	
	SPEI3	April	-0.067879078	
	SPEI3	May	0.076736782	
	SPEI3	June	0.155678899	
	SPEI3	July	0.097281601	
	SPEI3	August	0.013232926	
	t2m	March	-0.035380975	
	t2m	Aril	0.062824890	
	t2m	May	0.072232356	
	t2m	June	-0.111475131	
	t2m	July	-0.017854403	
	t2m	August	-0.016320094	

Appendix 3. List of drought years

Table A3. Drought years ranked by decreasing severity based on SPEI3 in June.

Site	Rank	Year	SPEI3 in June
E01-E04	1	1992	-2.35
	2	2018	-2.24
	3	1994	-1.69
	4	2023	-1.37
	5	1976	-1.25
	6	1989	-1.23
	7	1975	-1.21
	8	1969	-1.18
	9	1982	-1.05
	10	1986	-0.99
E05	1	1992	-2.21
	2	2018	-2.05
	3	2023	-1.93
	4	1994	-1.58
	5	1989	-1.44
	6	2008	-1.41
	7	1975	-1.33
	8	2006	-1.11
	9	1978	-1.03
	10	1967	-0.96

Appendix 4. Site-specific resilience indices

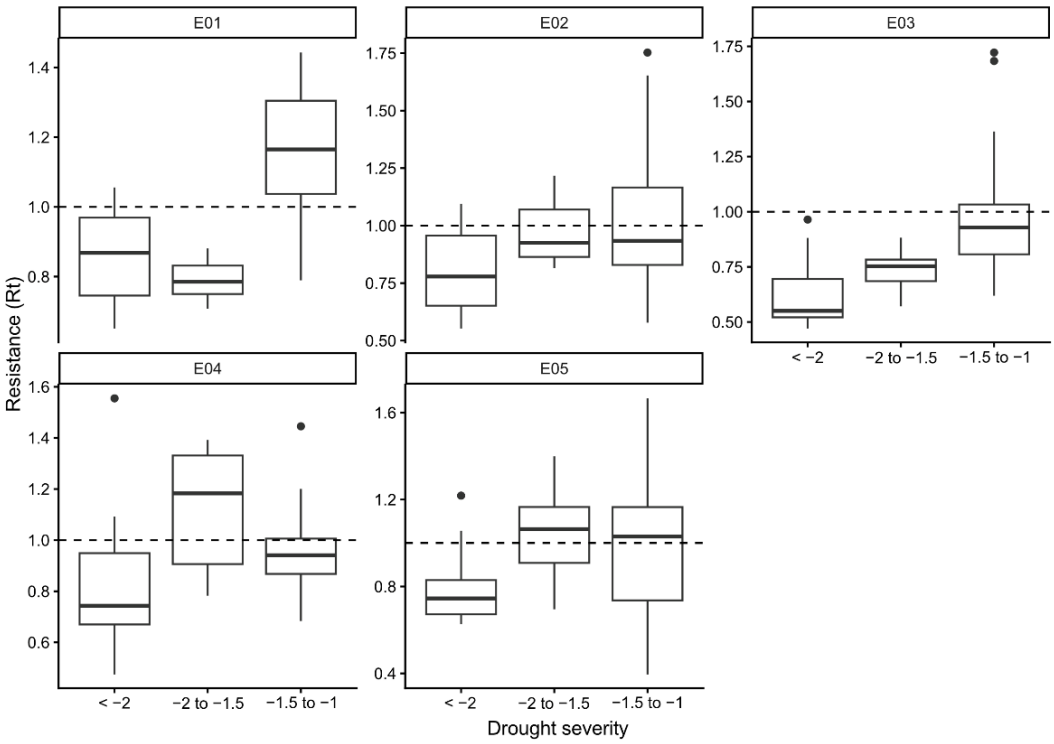

Figure A1. Resistance (Rt) across sites and drought severity classes. Indices are grouped by drought severity based on SPEI3 values (< -2.0 extreme, -2.0 to – 1.5 severe, -1.5 to -1.0 moderate). The boxes show distribution of resistance indices calculated from basal area increment at breast height (total of 26, 5 or 6 per site). The dashed horizontal line indicates Rt = 1 (no growth reduction relative to pre drought growth rates).

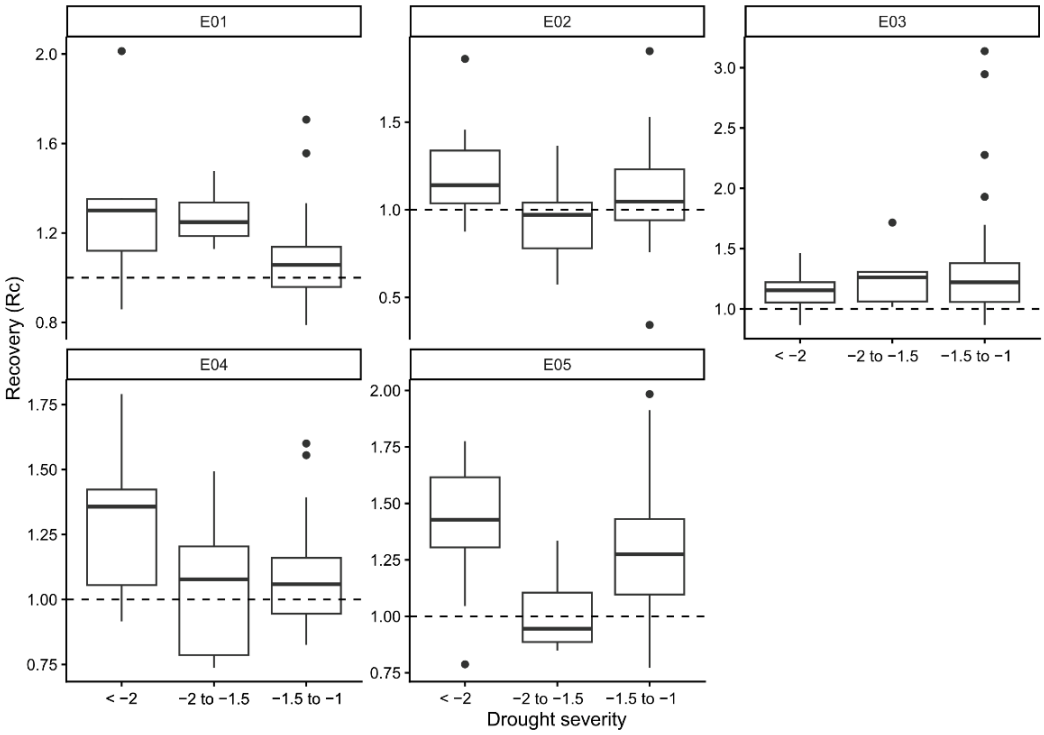

Figure A2. Recovery (Rc) across sites and drought severity classes. Indices are grouped by drought severity based on SPEI3 values (< -2.0 extreme, -2.0 to – 1.5 severe, -1.5 to -1.0 moderate). The boxes show distribution of recovery indices calculated from basal area increment at breast height (total of 26 tress, 5 or 6 per site). The dashed horizontal line indicates Rc = 1 (no return to pre drought growth rates).

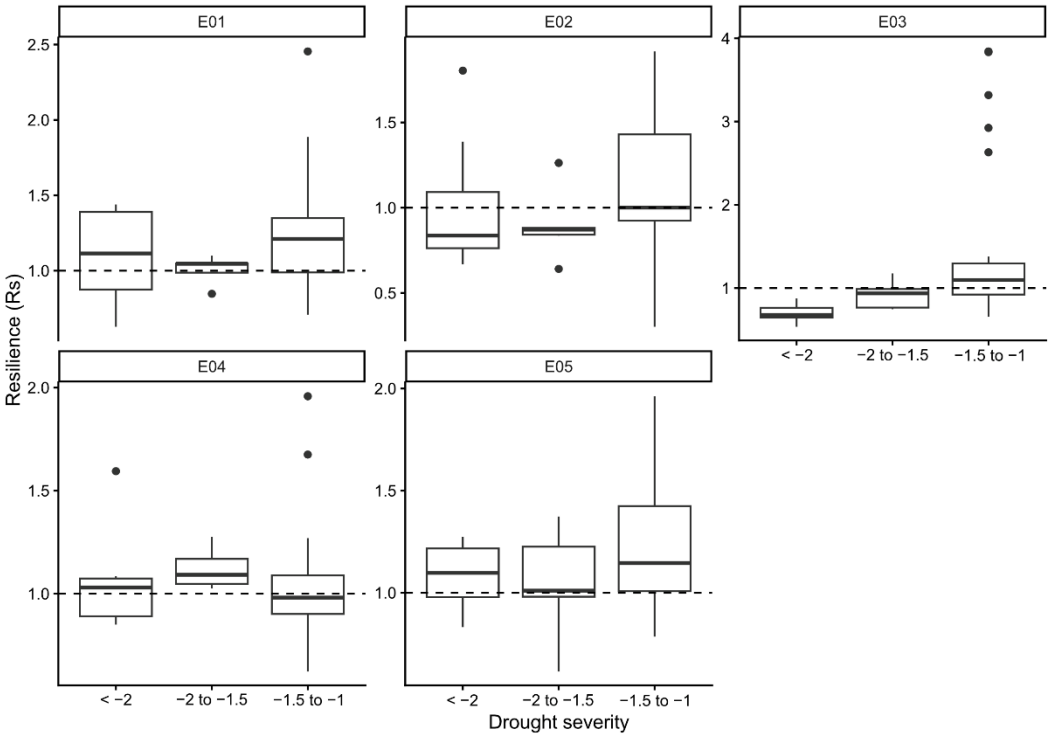

Figure A3. Resilience (Rs) across sites and drought severity classes. Indices are grouped by drought severity based on SPEI3 values (< -2.0 extreme, -2.0 to – 1.5 severe, -1.5 to -1.0 moderate). The boxes show distribution of resilience indices calculated from basal area increment at breast height (total of 26, 5 or 6 per site). The dashed horizontal line indicates Rs = 1 (growth after drought equals pre drought growth rates)

Appendix 5. Site-specific thresholds

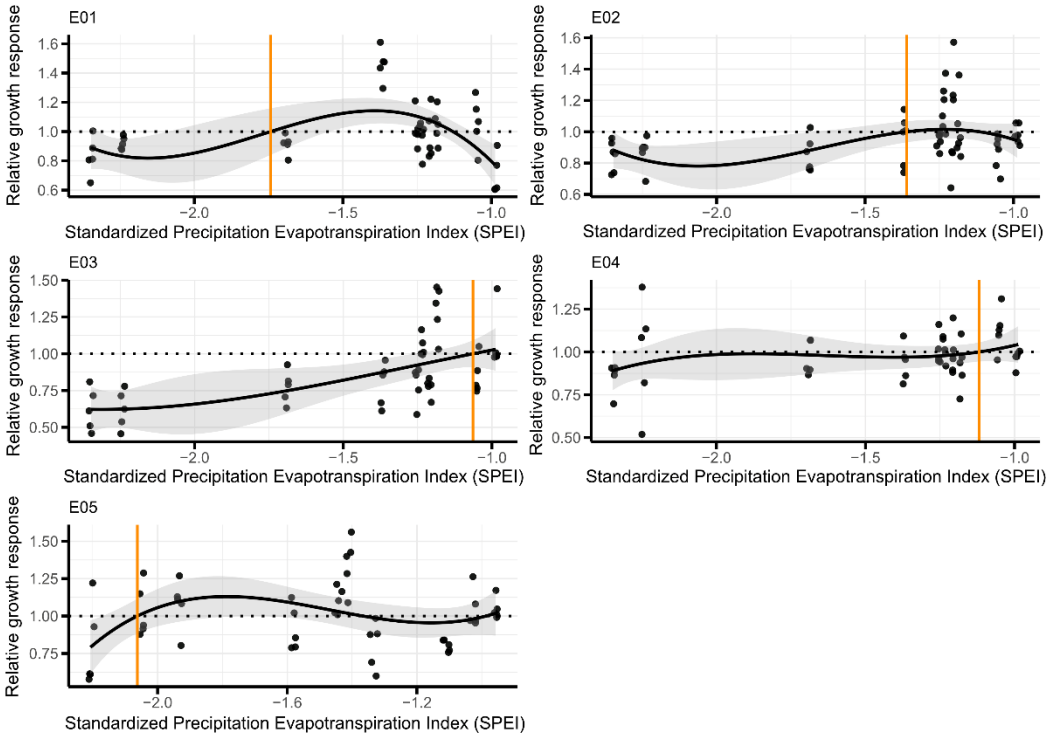

Figure A4. Oak relative growth response to drought intensity expressed with SPEI3 across study sites. Points represent growth responses of each tree (26) to 10 analysed drought events. Black lines show fitted response, dotted horizontal lines indicate no change in growth. Orange vertical line indicates drought thresholds when the fitted response (black line) crosses no response level (dotted line).

Appendix 6. Growth response to drought along the stem

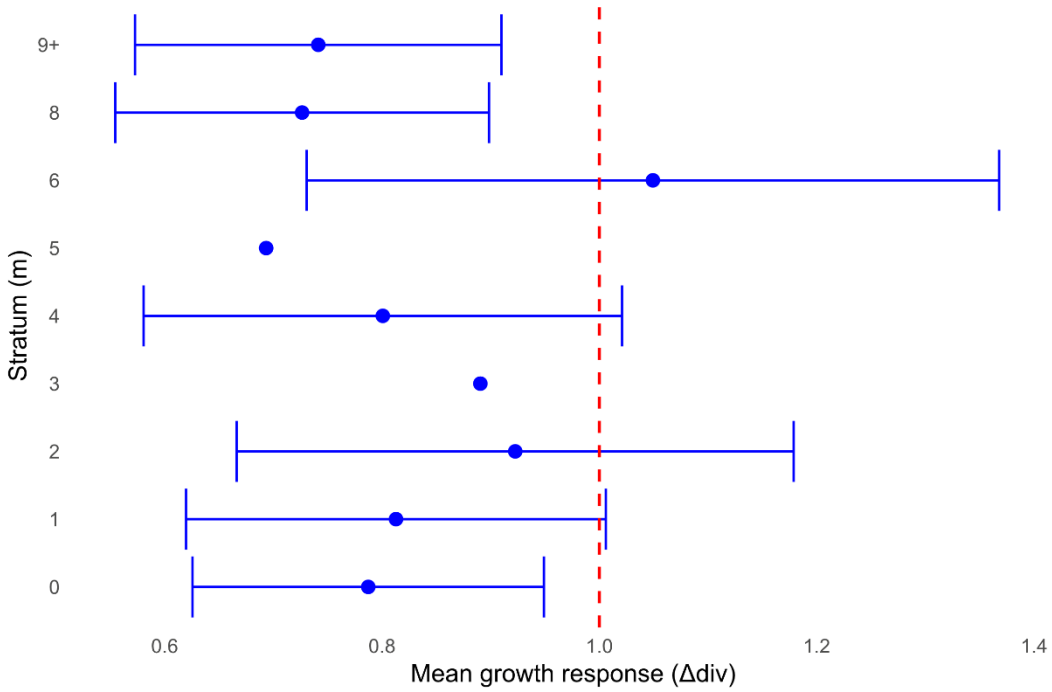

Figure A5. Vertical distribution of growth response (Δdiv) to drought along tree stems. Points represent the mean ration between projected and observed volume growth. Horizontal lines indicate 95% confidence intervals of the mean. The red dashed line indicates Δdiv = 1, corresponding to no deviation from the projected growth.

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