How leaf phenology impacts tree growth in a changing climate:

Case study of oak and beech trees in the Netherlands

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MSc Thesis in Environmental Sciences

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Environmental Systems Analysis

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Preface

During my thesis period, I expanded my understanding of tree growth dynamics in relation to climate change and enhanced my skills in RStudio. I found this time both fulfilling and enjoyable.

This would not have been possible without the contribution of several people, whom I would like to thank in this section.

First of all, I would like to thank both my supervisors Arnold and Jorad for their guidance, insights, and feedback. I especially want to thank Arnold for providing phenology data and Jorad for his extensive support with RStudio and for making the FSTree model available to me.

Additionally, I would like to thank Paul for his time, effort and ideas in the proposal phase. I would also like to thank him for bringing me in touch with Jorad and providing tree radial growth data.

I am also grateful to my fellow thesis students - Alfred, Anna, Emilia and Circe – who made this journey more enjoyable and successful with our regular coffee breaks, motivation and feedback. In addition to this, I like to thank Sverre for organizing the thesis ring and providing coffee and cookies during the thesis ring coffee break.

Last but not least, I would like to thank my friends and family for their support, interest and stress-relieving activities. A special thanks to Bart, Esther, Klais, Aniek, Stephanie and Chuan.

Abstract

Climate change affects forests; however, there are still many uncertainties, especially how it affects specific species in specific regions. Key indicators of impacts of climate change on forests are shifts in leaf phenology, which potentially affect tree radial growth. Pedunculate oak (Q*uercus robur*) and European beech (*Fagus sylvatica*) are prevalent deciduous tree species in the Netherlands, however the link between changes in phenology and radial growth in these species remains underexplored, particularly in light of the KNMI's recent climate change scenarios. Therefore, the objective of this research was to gain a better understanding of the effects of global warming on the growth dynamics of Pedunculate oak and European beech in the Netherlands. I conducted Pearson correlation tests and linear mixed models in RStudio to assess relationships between historical climate data, historical leaf unfolding data, and historical tree radial growth data. Additionally, I used the FSTree model, which simulates the growth of individual trees in a forest plot, to predict future timing of leaf unfolding and radial growth in beech under different climate change scenarios.

The analysis showed that April temperatures had the strongest correlation with leaf unfolding in both oak (-0.788) and beech (-0.795), indicating that warmer temperatures in April lead to earlier leaf unfolding. There was a significant negative correlation between the day of leaf unfolding and radial growth in oak (-0.424), whereas for beech this correlation was positive (0.462), indicating that earlier leaf unfolding leads to increased radial growth for oak and reduced radial growth for beech. The FSTree model predicts that leaf unfolding of beech will occur earlier and radial growth will decline in the future under all climate change scenarios, with the greatest advancement and decline under the most extreme scenario (SSP5) and the least under the mildest scenario (SSP1). Under the SSP5 scenarios, earlier leaf unfolding is anticipated to lead to an even bigger decline in radial growth in beech. A potential explanation for this is a shift in resource allocation from wood production to increased reproduction, however, this hypothesis was tested, and the results indicated an overall decrease in biomass production rather than a change in allocation patterns. Therefore, the hypothesis is rejected.

The reliability of the leaf unfolding data is affected by the method of data collection, as the data was obtained by volunteers. Furthermore, the radial growth and leaf unfolding data were unpaired, and variations in tree age and location were not considered. Nevertheless, the findings offer valuable insights into the overall growth dynamics of oak and beech trees in the Netherlands. Lastly, the model did not simulate oak, leaving a gap in the understanding of their potential future growth.

In conclusion, the strong dependency of leaf unfolding on April temperatures suggests that global warming will lead to earlier leaf unfolding, nevertheless, especially beech may become increasingly reliant on chilling and photoperiod requirements, though the extent of this shift remains uncertain. Further research is needed to clarify why beech may experience reduced radial growth with earlier leaf unfolding, while the opposite relationship is found in oak.

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Glossary

Abbreviation / Concept	Definition
Allocation	Partitioning of carbohydrates to various sinks (trunk, branches, roots etc.).
Assimilates	Carbohydrates (e.g. sugars) from photosynthesis.
End of growing season	Leaf coloration and fall in autumn.
GDD	Growing Degree Days (sum of average daily temperature minus a base temperature).
LU	Leaf Unfolding
SPEI	Standardized Precipitation Evapotranspiration Index (difference between precipitation and evapotranspiration).
SSP	Shared-Socio economic Pathways - Climate scenario's IPCC
Start of growing season	Leaf unfolding in spring
Tmax	Maximum temperature
Tmin	Minimum temperature
TRavg	Average tree radial growth

1. Introduction

1.1 Problem statement and background

Climate change has profound impacts on forests; many current climates will become unsuitable for existing species, leading to major shifts in species distribution and composition of forests by 2100 (Lindner et al., 2014). Additionally, an increase in disturbances, such as droughts, wildfires and outbreaks of diseases and insects is expected (Linder et al., 2014). The severe summer drought of 2018 in Europe caused tree mortality across many species and several trees did not recover from the drought by 2019, leaving them more vulnerable to disturbances like insect outbreaks (Schuldt et al., 2020). Such insect outbreaks cause damage to trees, for example bark beetle outbreaks cause trees to emit carbon rather than sequestrating it, contributing to climate change instead of mitigating it (Brockerhoff et al., 2017; Allen et al., 2010; Brück-Dyckhoff et al., 2019). Finally, forest productivity is likely to change, with its extent and direction varying depending on the type of forest, area and the severity of climate change (Sperlich et al., 2020; Spathelf et al., 2013). These collective findings emphasize the vulnerability of forests to climate change; however, there are still many uncertainties, such as responses of specific species in specific regions. Maintaining healthy forests is important to protect forest ecosystem services and biodiversity, making it essential to research the impact of climate change on forests (Lindner et al., 2014).

One of the key indicators of the impacts of climate change on forests are shifts in leaf phenology, which studies the timing of biological recurring events and their relation to biotic and abiotic factors. These shifts may potentially affect tree growth, making them important to study in more detail (Schmidt et al., 2014; Verma et al., 2022; Li et al., 2023). Factors such as temperature, water availability and day length influence the timing and length of the growing season (Verma et al., 2022; Schmidt et al., 2014), with temperature being the main factor in temperate climates (Vitasse et al., 2011; Didion-Gency et al., 2023). Increased temperatures result in an earlier start of the growing season, but may lead to a shorter growing season overall (Li et al., 2023; Hurbedise et al., 2019). Climate change affects the timing of leaf unfolding in spring to a greater extent than the leaf senescence in autumn (Chen et al., 2018). For this reason, this research focuses on the impacts of climate change on the timing of leaf unfolding.

Pedunculate oak (Q*uercus robur*) and European beech (*Fagus sylvatica*) are two of the most common deciduous tree species in the Netherlands (Schelhaas et al., 2002; Vodde et al., 2005). Changes in the growing season of these tree species can affect the production of acorns and beechnuts impacting both tree reproduction and food availability for certain animal species (Journé et al., 2021; Nussbaumer et al., 2021). Furthermore, phenology shifts can impact species interactions, alter water and carbon cycles and make trees more susceptible to frost damage in early spring (Cole & Sheldon, 2017; Fang et al., 2022). Shifts in phenology can also affect tree radial growth, which is an indicator for forest productivity and thus for its health and survival (Vannoppen et al., 2020). Radial growth depends on several factors, with the main factors being, temperature, water and light availability (Scharnweber et al., 2013; Chakraborty et al., 2021; Kang et al., 2023). Under warmer and dryer conditions, gross primary productivity of trees decreases, resulting in less tree radial growth (Van Der Woude et al., 2023). Although European beech is likely to be more susceptible to climate change, the Pedunculate oak has also experienced growth decline due to an increase in drought events (Meyer et al., 2020; Losseau et al., 2019).

The relationship between changes in tree phenology and radial growth varies across regions and species, with a lack of studies specifically focusing on oak and beech in the Netherlands (Kang et al., 2023; Dox et al., 2022; Stridbeck et al., 2022; Didion-Gency et al., 2023; Etzold et al., 2021). Additionally, most existing studies focus on general climate change projections, but climate change varies by region, so it is crucial to use regional climate change scenario data with specific climate variables that affect tree growth (Lindner et al., 2014). The Royal Netherlands Meteorological Institute (KNMI) has developed new climate change scenarios (KNMI – KNMI'23: klimaatscenario's voor Nederland, 2023) that have not yet been utilized in researching the specific impacts of climate change on the growth dynamics of trees in the Netherlands. As a result, the impact of changes in phenology on the radial growth of oak and beech trees in the Netherlands and its future predictions remain underexplored. This gap can be addressed by leveraging the newly developed scenarios from the KNMI and therewith valuable insights into growth dynamics of Dutch forests can be provided.

1.2 Objective and research questions

The objective of this thesis is to gain a better understanding of the effects of global warming on the growth dynamics of Pedunculate oak and European beech trees in the Netherlands. This includes the impact of climate change on the start of the growing season, the relationship between the start of the growing season and radial growth and predictions of changes in growth patterns under future climate change scenarios.

This objective leads to the following research questions (RQs) that will be answered:

1. How does temperature affect the start of the growing season of oak and beech trees?
2. What is the relation between the start of the growing season and radial tree growth?
3. How are the start of the growing season and radial tree growth expected to change under the future climate change scenarios?

2. Methods

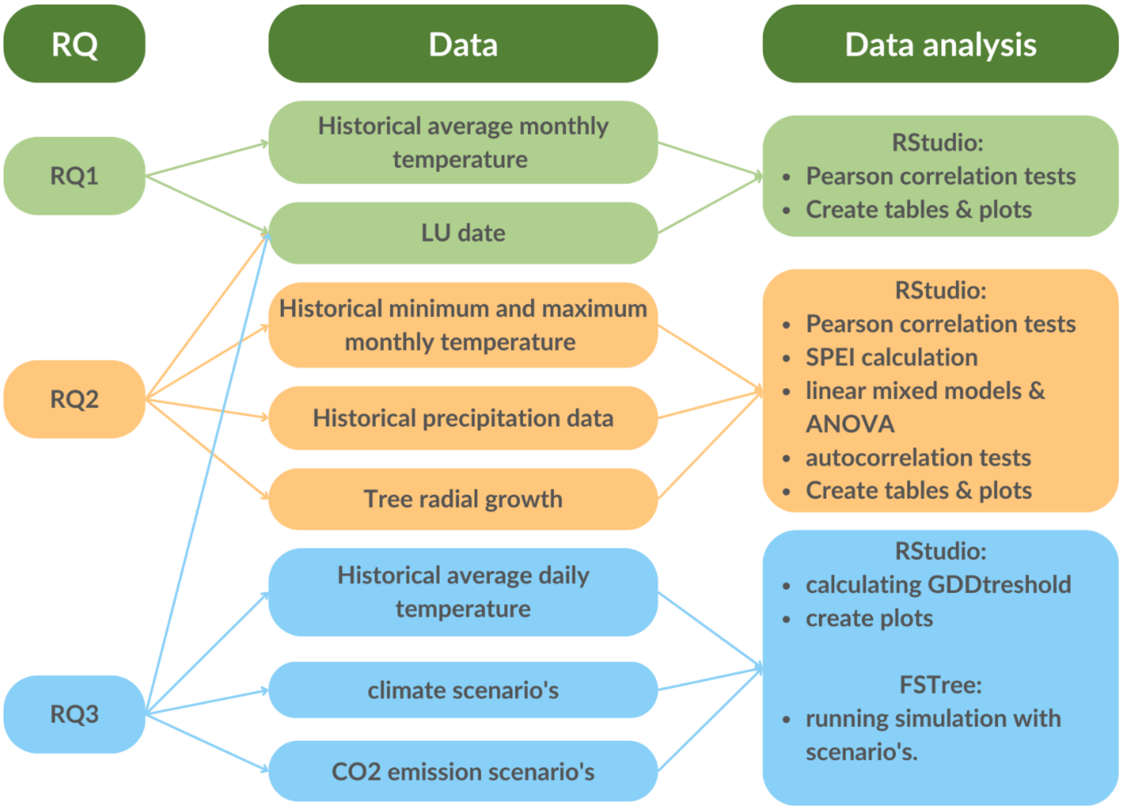

Figure 1 – Overview of the data used and the data analysis per Research Question (RQ), with green being used for RQ1, orange for RQ2 and blue for RQ3. LU = leaf unfolding, SPEI = Standardized Precipitation Evapotranspiration Index, ANOVA = Analysis Of Variance and GDD = Growing Degree Days.

2.1 Data

This section delves into the climate data, phenological data and tree growth data used in this research. For a brief overview of all the data used in this study, see Figure *1* and Table *1* in appendix 9.

2.1.1 Climate data

For this study I used the historical daily average, monthly average, monthly minimum and maximum temperature and historical precipitation data from the year 1901 onwards (KNMI - *Maand- En Jaarwaarden*, 2024). All climate data were from the weather station in De Bilt, as this is centrally located in the Netherlands and thus representative for the Dutch average (KNMI – *automatische weerstations*, 2024).

Additionally, I used transformed time series for the climate change scenarios for the third RQ, developed by the Royal Netherlands Meteorological Institute (KNMI). The dataset of the time series 1990 to 2020 was transformed to the time series of 2085 to 2115 (KNMI – *klimaatscenarios,* 2024). The following scenarios were developed by the KNMI (KNMI – *KNMI'23: klimaatscenario's voor Nederland*, 2023) (see Figure *2*):

- Hd: high CO_2 emissions (SSP5-8.5) and drying.
- Hw: High CO_2 emissions (SSP5-8.5) and wetter.
- Ld: Low CO_2 emissions (SSP1-2.6) and drying.
- Lw: Low CO_2 emissions (SSP1-2.6) and wetter.

For the two high CO_2 emissions scenarios (Hd and Hn) the average annual temperature in the Netherlands will keep rising at least until 2100. For the two low CO_2 emissions scenarios (Ld and Ln), the temperature will keep rising until 2050, after that the temperature will remain stable, but is still higher than the current annual average temperature.

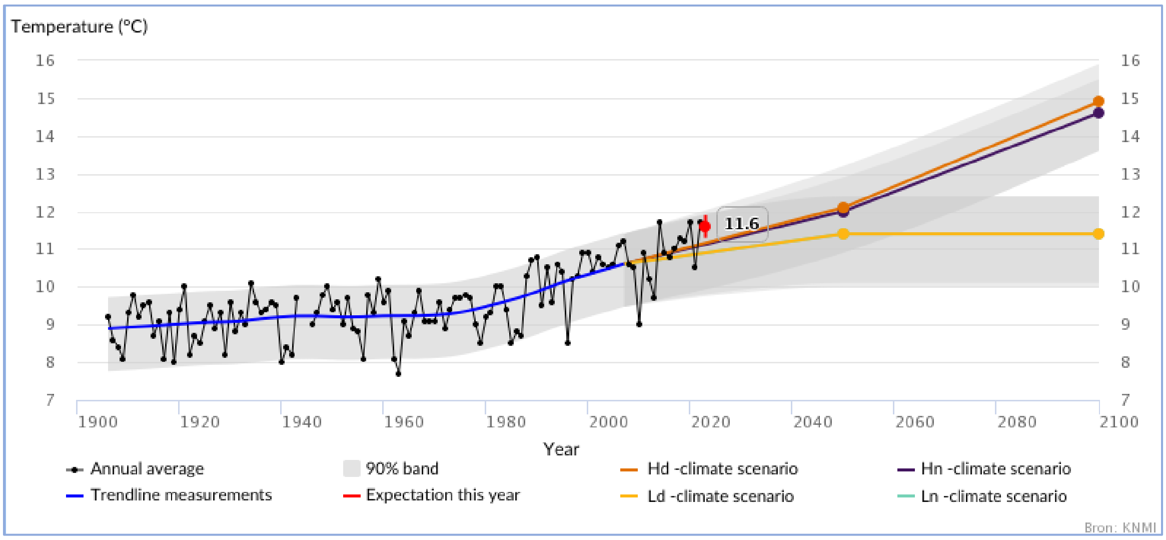

Figure 2 - Average annual temperatures in the Netherlands in the past and for the four different climate scenarios until 2100. With orange representing the Hd-scenario = High CO2 emisisons and dry, purple is Hn scenario = High CO2 emissions and wet, yellow is Ld scenario = Low CO2 emissions and dry and light blue is Ln = Low CO2 emissions and wet. The black lines and dots represent historical annual average temperatures, with the blue line being the trendline for the historical annual average temperatures. The red dot and line, with the number 11.6, represent the expected average temperature for this year (2024). The grey 90% band indicates the range within which 90% of the average annual temperatures (are expected to) fall– Adapted from KNMI – *Klimaatdashboard* (2023).

The high and low CO_2 emissions are based on the scenarios of The Intergovernmental Panel on Climate Change (IPCC). Shared Socio-economic Pathways (SSP) are climate change scenarios describing socio-economic shifts, containing predictions for greenhouse gas emissions. For the SSP1 scenario the CO_2 emissions are expected to decline from around 40 Gigatonnes per year to a bit below zero by 2100. For the SSP5 scenarios an increase to about 125 Gigatonnes CO_2 emissions per year is expected (IPCC, 2023).
The KNMI considers a wet climate projection where winters will be extremely wet and summers slightly drier, and dry scenarios where winters will be slightly wetter and summers extremely dry (KNMI – *KNMI'23: klimaatscenario's voor Nederland*, 2023).

To be able to distinguish between the effect of CO_2 and the combination of temperature and precipitation on the leaf unfolding day and tree radial growth, a distinguish was made between SSP5 with high and low CO_2 emissions (IPCC, 2023). This resulted in the following six scenarios used for RQ3: SSP1 Wet, SSP1 Dry, SSP5 Low CO_2 Wet, SSP5 Low CO_2 Dry, SSP5 High CO_2 Wet, SSP5 High CO_2 Dry (see Table *1*). So, in the SSP5 low and high scenarios, the only difference was the CO_2 concentration, temperature and precipitation were unchanged. See Table *1* in appendix 9 for a complete overview of the data.

2.1.2 Phenological data

I used historical phenological data of oak and beech trees in the Netherlands from the Natuurkalender project, collected by volunteers (Nature Today, n.d.). The data was collected at different locations in the Netherlands between 1900 and 2023, with missing data between 1969 and 2001 (32 years). As the data were collected by volunteers, the individuals on which data was collected and the total number of observations vary from year to year. The data consists of different phenophases, such as leaf unfolding (LU) and leaf colouring, each datapoint contains the date on which the phenophase was observed. I only used the LU date, as this research only focuses on the start of the growing season (see Table *1* for an overview of the data).

2.1.3 Tree growth data

Historical tree radial growth data of oak and beech trees in the Netherlands were collected from 15 oak and 15 beech trees in the Pijpebrandje Forest Reserve located near Ermelo (Dendrochronology lab Wageningen University & Research). There is data available from 1862 until 2020 for the beech and from 1832 until 2020 for the oak. Dendrochronology's of two cores per tree were taken, this means that there are two data points for each tree (in the years that the tree existed), of which I took the average, so that there was one data point per tree left (see Table *1* for an overview of the data).

2.2 Data analysis

For the first two research questions I used RStudio for the data analysis and for the third research question I additionally used the FSTree model.

2.2.1 RQ1

To determine how the start of the growing season of Pedunculate oak and European beech trees are affected by temperature, I analysed historical temperature data and historical phenology data in RStudio. First, I did some data preparation. Only LU was selected of the phenophases and wrong observations (after June) were removed from the LU data. After converting the LU date from a date format (day/month/year, e.g. 21/04/2015) to the Julian day (e.g. 111) with the year in a separate column, I calculated the average LU date of both beech and oak. Then, I moved the temperatures for the months after the LU date (June until December) to the year after, as these temperatures might affect the LU of the next year. After data preparation, I created plots to get insight in the data, such as the average yearly temperature over the years. The LU date (of both beech and oak) was merged with the temperature dataset to be able to perform Pearson correlation tests between the temperature in each month and the LU date. As the temperature in almost all months was correlated to the LU date and highest for April, I performed correlation tests of the temperature in April and the other months to test for autocorrelations.

2.2.2 RQ2

To be able to investigate the relationship between the growing season and tree radial growth, I took the average of the two cores per tree and the average of all trees and determined the Pearson correlation with LU.

The LU date is affected by the temperature in certain months, therefore tests needed to be done to determine whether the correlation between LU and tree radial growth is not actually a correlation between temperature and tree radial growth. Radial growth is strongly affected by drought, which depends on both temperature and precipitation (Del Castillo et al., 2022). Therefore, I used minimum (Tmin) and maximum (Tmax) monthly temperatures to calculate the Standardized Precipitation Evapotranspiration Index (SPEI), which is the difference between the amount of precipitation and the amount of evapotranspiration, so it takes both temperature and precipitation into account (KNMI - *Achtergrondinformatie Neerslagindexen SPI En SPEI*, 2024). I performed Pearson correlation tests between the SPEI and the average tree radial growth after merging SPEI with the average tree radial growth.

After combining precipitation, Tmin and Tmax for three months, I calculated the SPEI for three months and did correlation tests between SPEI in three months and radial growth.

I performed Linear mixed models to test which variables explain the tree radial growth the best, with the average tree radial growth (TRavg) as dependent variable and SPEI the independent variable. SPEI for three months was taken to prevent overfitting, with SPEI in April-June as basis for beech (m1). For each next model, I added the SPEI of certain months (m2, m3, m4) and tested the average radial growth in an "empty" model, as control model (m5), resulting in the following models:

$$m1 < -lm(TRavg \sim AprJun, data = merged\_SPEI\_TRB\_LU)$$

$$m2 < -lm(TRavg \sim AprJun + JulSep, data = merged\_SPEI\_TRB\_LU)$$

$$m3 < -lm(TRavg \sim AprJun + JulSep + OctDec, data = merged\_SPEI\_TRB\_LU)$$

$$m4 < -lm(TRavg \sim AprJun + JulSep + OctDec + JanMar, data = merged\_SPEI\_TRB\_LU)$$

$$m5 < -lm(TRavg \sim 1, data = merged\_SPEI\_TRB\_LU)$$

With these models, I performed several Analysis Of Variance (ANOVA) tests to compare the different linear mixed models. I applied the same linear mixed models for oak trees, but then with the SPEI in January until March as basis (m1).

I added the LU day to the model that performed best, creating m6 and performed another ANOVA test.

$$m6\ (beech) < -lm(TRavg \sim AprJun + JulianDayLU, data = merged\_SPEI\_TRB\_LU)$$

$$m6\ (oak) < -lm(TRavg \sim JanMar + JulianDayLU, data = merged\_SPEI\_TRB\_LU)$$

Lastly, I tested for autocorrelations between SPEI in April until June and the LU day, SPEI in January until March and the LU day and between SPEI in the different months. The threshold for autocorrelations was 0.2, when this value was exceeded it was considered as autocorrelated (see the blue horizontal line in Figure *11* and Figure *12* in appendix 10.2).

2.2.3 RQ3

To explore how tree phenology and tree radial growth are expected to change in the future, I did a simulation in the FSTree model. The model simulates the growth of individual trees in a forest plot, based on their morphology and physiology and can predict responses of individual trees in a forest to different climatic conditions (de Vries et al., in prep.). This makes the model particularly suitable to test how the growing season and tree radial growth are expected to change under the different climate change scenarios. The model was developed in the modelling platform GroImp, for a more detailed explanation of the model, see de Vries et al. (in prep).

The model simulates the European Beech *(Fagus sylvatica)* (de Vries et al., in prep.), but not the Pedunculate oak, thus future predictions of the phenology and radial growth could not be tested for the oak. For beech trees, I did the following simulation:

I used a fixed and temperature-dependent LU date and the six different scenarios as model inputs: SSP1 Wet, SSP1 Dry, SSP5 L Wet, SSP5 L Dry, SSP5 H Wet, SSP5 H Dry (see Table *1*). By running this simulation, the impact of the different scenarios on the temperature-dependent LU date and tree radial growth could be tested. For the fixed LU date, I took the average LU date of the phenology data, which was Julian day 117.

I made The LU date temperature-dependent by making use of the Growing Degree Days (GDD), GDD is the sum of the average daily temperatures (Td) from a certain date onwards, minus a certain base temperature (Tbase). When the daily temperature minus the base temperature is below zero, zero will be added to the overall GDD, instead of a negative number (Wenden et al., 2019). This results in the following general formula for GDD, where GDD is the sum of GDD between the start day (dstart) and day n (Wenden et al., 2019):

$$\left(\sum GDD\right)_n = \sum_{d=dstart}^{n} \max\left(0, T_d - T_{base}\right)$$

First, a function in RStudio was created to calculate the threshold GDD, which is reached on the day of LU, for all LU data. The base temperature was set to 5°C and the start date was set to the first of January (Dantec et al., 2014; Dox et al., 2022; Fu et al., 2016; Wenden et al., 2019). To calculate the threshold GDD of each LU observation, I utilized the daily mean temperature data of the KNMI. The output was a distribution shown in a histogram with the threshold GDD of each LU observation, of which I calculated statistics (i.e. mean, median and standard deviation).

The skewness of the distribution was 0.44 according to the following formula:

$$Pearson's\ median\ skewness = 3x\,\frac{(Mean - Median)}{Standard\ deviation}$$

As this outcome is higher than the boundary of 0.4, the distribution is right skew. This means that the median threshold GDD is more accurate than the mean threshold GDD, as more data points are on the left side of the mean due to the skewness (Doane et al., 2011). For this reason, I used the median threshold GDD (184.8) as input for the simulation with the temperature-dependent LU date in the FSTree model.

The following equation was used in the FSTree model to make the LU date temperature-dependent:

$$GDD_t \leq \sum_{d=d_{start}}^{d_{LU}} \left(\min(0, T_d - T_{base})\right)$$

GDD_t is the threshold GDD, d_{LU} is the day of LU, T_d is the average daily temperature on day d from the start day (d_{start}, 1st of January) and T_{base} is the base temperature (set to 5°C). The equation calculates GDD and once GDD is greater than or equal to the threshold GDD, the day of LU is reached. The end date of the growing season was a fixed date (Julian day 305) in the simulation.

After running the simulation, I calculated the average LU date and tree radial growth per year per scenario per treatment, because averages were used in RQ1 and 2 as well. As there was no difference between the dry and wet scenarios, the wet scenarios were removed from the plots.

Due to the outcome of the simulation, which implied a decline in tree radial growth if LU advances, an extra analysis was performed with the output of the FSTree model to test the following hypothesis: A change in LU coincides with a change in peak cambial activity to before the seasonal peak in photosynthetic yield. Consequently, more assimilates are allocated towards reproduction than towards cambial growth. See chapter 5 for a more detailed explanation.

To test whether there was a shift in allocation, I calculated averages for the total wood biomass, the wood production, storage and seed production per scenario and per treatment. With these averages I calculated the ratio between the wood production and seed production and the ratio between the storage and total wood biomass, to correct for tree size. The allocation ratio between wood and reproduction is expected to decrease with an earlier leaf unfolding day.
Lastly, the same steps were repeated, but then calculating the averages per tree, per scenario and per treatment to be able to compare the wood-to-seed production ratio in boxplots.

3. Influence of temperature on timing of leaf unfolding

For oak, there was a negative correlation between the day of LU and the temperature in each month, whereas for beech, this correlation was absent for October of the previous year (see Table 3 and Table 2 in appendix 10.1 respectively). An increase in April temperatures correlated most strongly with an earlier day of leaf unfolding for both beech (r = -0.795, P < 0.001) and oak (r = -0.788, P < 0.001) (see Table 2 and Table 3 in appendix 10.1 respectively and Figure 3).

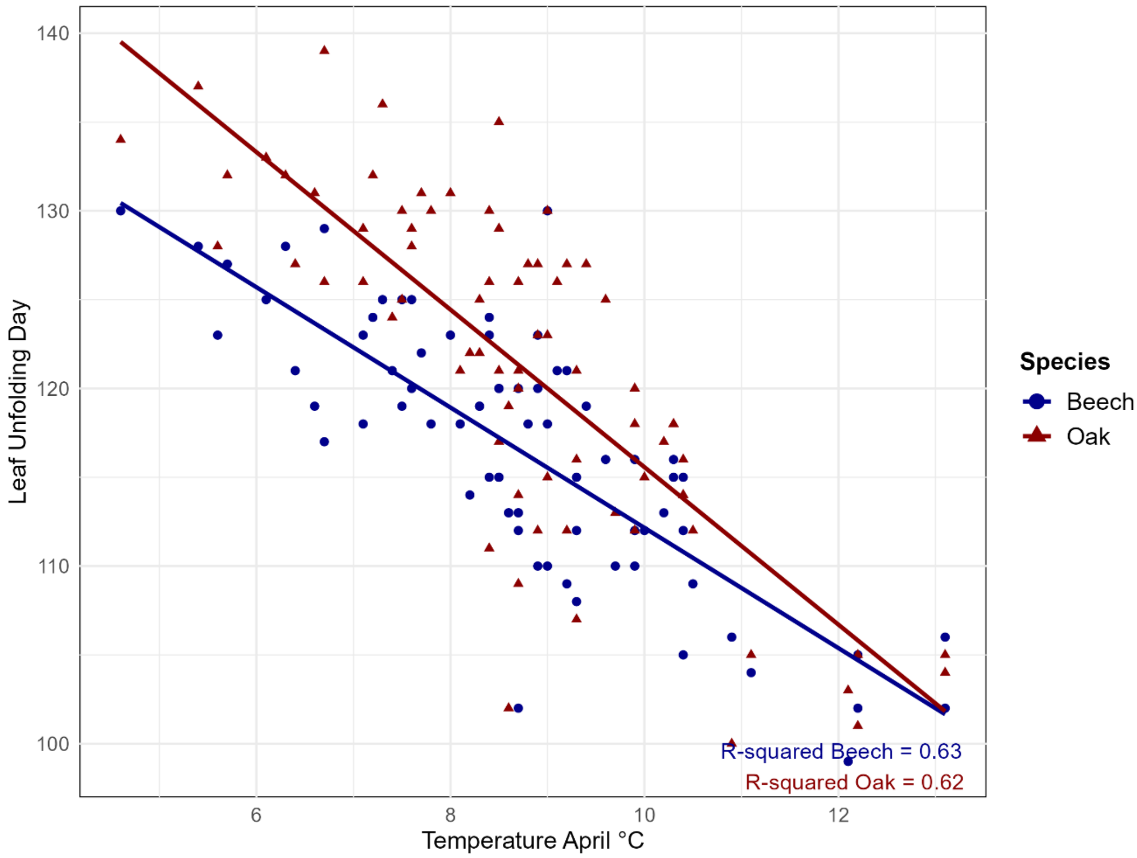

Figure 3 - Plot of the leaf unfolding day (Julian Day) on the y-axis and the temperature in April on the x-axis, showing the trendline and the R-squared for oak (red triangles) and beech (blue circles).

There was a significant correlation between the temperature in April and all other months, except for May, October and December (see Table 4 in appendix 10.1). Long-term trends of increasing temperatures (Figure 10 in appendix 10.1), affect the temperature during the entire year, causing autocorrelations between temperatures in different months of the same year. For this reason, the correlations between the temperature in the other months and the LU date are due to autocorrelations and thus not taken into account.

4. Relation between timing of LU and radial growth

For beech an earlier LU date results in less tree radial growth (r = 0.462, P < 0.001), whereas for oak the opposite is true (r = -0.424, P < 0.001) (see Figure *4*).

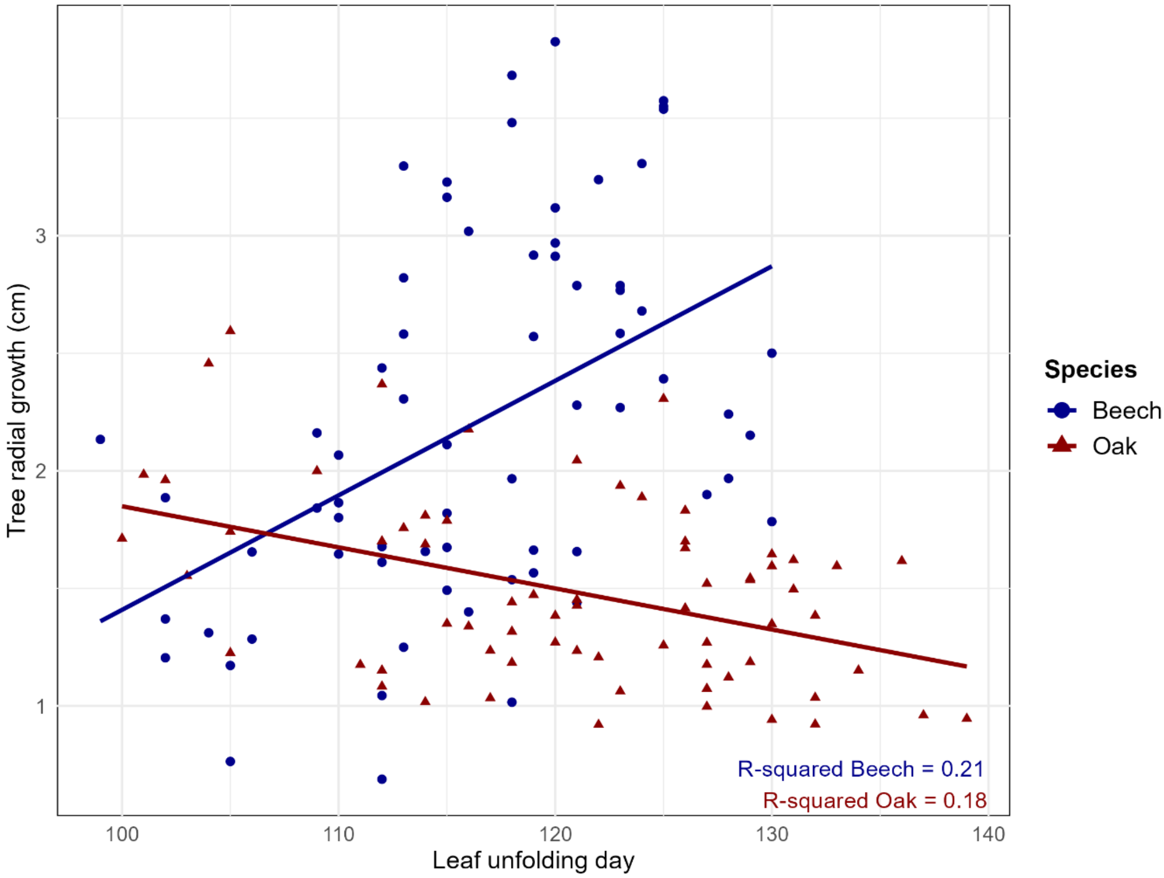

Figure 4 – plot of leaf unfolding day on the x-axis and tree radial growth on the y-axis, showing the trendline and R-squared for oak (red triangles) and beech (blue circles).

To test whether the correlation between LU and tree radial growth was not actually a correlation between the temperature and radial growth, first the correlation between radial growth and SPEI was tested. The tree radial growth of beech positively correlated with the SPEI in the months April, May and June (see Table 5 in appendix 10.2). Also, a higher value for SPEI of three months for April until June results in more radial growth of beech (r = 0.245, P < 0.01) (see Table 6 in appendix 10.2 and Figure 5).

For oak, the correlation coefficients of the radial growth and SPEI in the months April, September and October were the highest and significant (see Table *12* in appendix 10.2). However, the radial growth correlated strongest to the SPEI of three months for January until March (r = 0.309, P < 0.001) (see Table 13 in appendix 10.2), so the SPEI of these three months was taken for oak trees and plotted against the tree radial growth (Figure *5*).

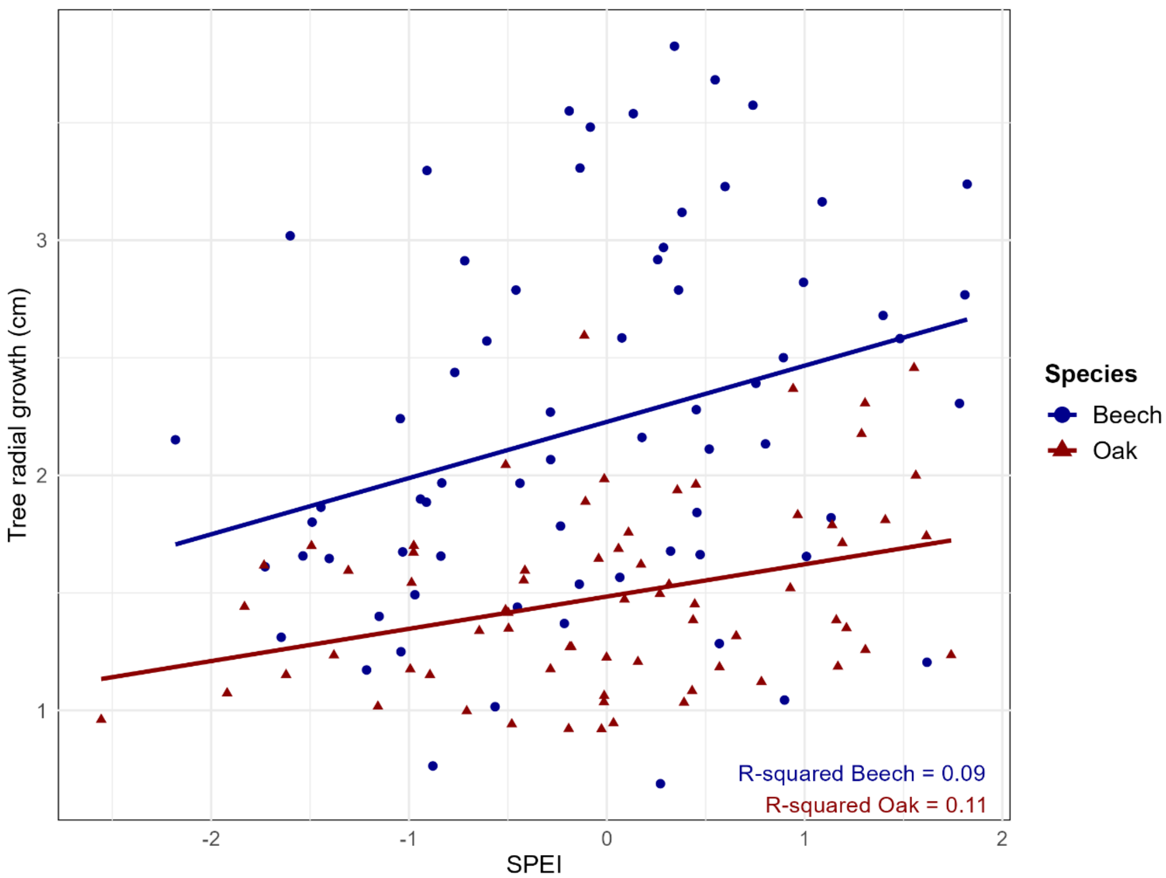

Figure 5 - plot of SPEI of April until June for beech (blue circles) and SPEI of January until March for oak (red triangles) on the x-axis and tree radial growth on the y-axis, showing the trendline and R-squared.

There were no autocorrelations between SPEI in April until June and the other months and between SPEI in January until March and the other months (see Table 7 and Table 14 in appendix 10.2 respectively).

From the linear mixed models with solely SPEI as factor, the model with SPEI in April until June (m1) and the model with SPEI in January until March (m1) were the only significant models for beech and oak respectively (see Table *8*, Table *9*, Table *10*, Table 15, Table *16* and Table *17* in appendix 10.2). Therefore, LU was added as extra factor to these models. The models with SPEI in three months and the LU day as independent variables (m6) had lower P-values than the models with only SPEI of three months as independent variable (m1) (Table *11* and Table 18 in appendix 10.2 for beech and oak respectively). There were no autocorrelations between SPEI in April until June and the LU date and between SPEI in January until March and LU date, so it was not due to autocorrelations that these models performed best (see Figure 11 and Figure 12 in appendix 10.2 respectively). This indicates that the combination of LU date and SPEI in April until June for beech and the combination of LU date and SPEI in January until March for oak (m6) explain the tree radial growth the best.

5. Future changes in LU date and radial growth under global warming

The LU of beech is expected to advance most for the high greenhouse gas emission scenarios (SSP5) and least for the low emission scenario (SSP1) compared to the current situation and fixed LU date (see Figure 6). In the current situation the fixed and temperature-dependent LU are quite similar, because the fixed LU date is the average of the past century and the temperature-dependent LU for the current situation is based on temperatures of the past decades. In the SSP1 scenario, the temperature rises only slightly, resulting in a minor difference in the temperature-dependent LU compared to the current situation. The LU patterns in the SSP5 scenarios are similar, as the only differing factor is the level of CO_2 and in the model LU solely depends on temperature.

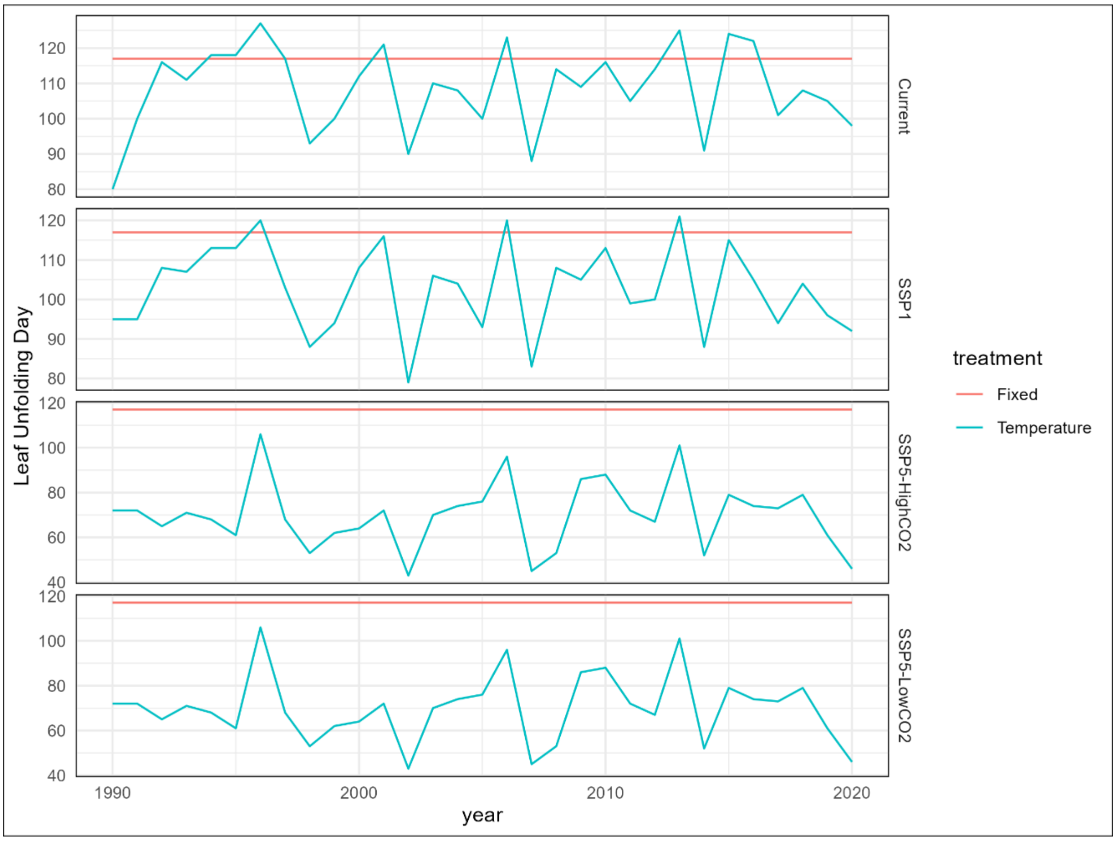

Figure 6 – Changes in a temperature-dependent leaf unfolding date (blue) under different climate change scenarios, compared to the fixed leaf unfolding date (orange) (day 117, average LU of past decades).

The radial growth of beech is expected to decrease in the future for each scenario and for both a fixed and temperature-dependent LU compared to the current situation (see Figure 7). In the low emission (SSP1) scenario, being mainly warmer and dryer than the current situation, a similar decrease in radial growth is expected under both a fixed and temperature-dependent LU. Compared to the SSP1 scenario, the radial growth is expected to decrease in the even warmer and dryer SSP5 scenarios, with a bigger decrease in the low emission SSP5 scenario, indicating that CO_2 concentration affects radial growth. In line with the findings of chapter 4, in both SSP5 scenarios, a bigger decrease in the radial growth is predicted under a temperature-dependent LU than under the fixed LU. In short, a decline in tree radial growth is expected under warmer and dryer conditions, reduced CO_2 concentrations within the SSP5 scenario and the advancement of LU in both SSP5 scenarios.

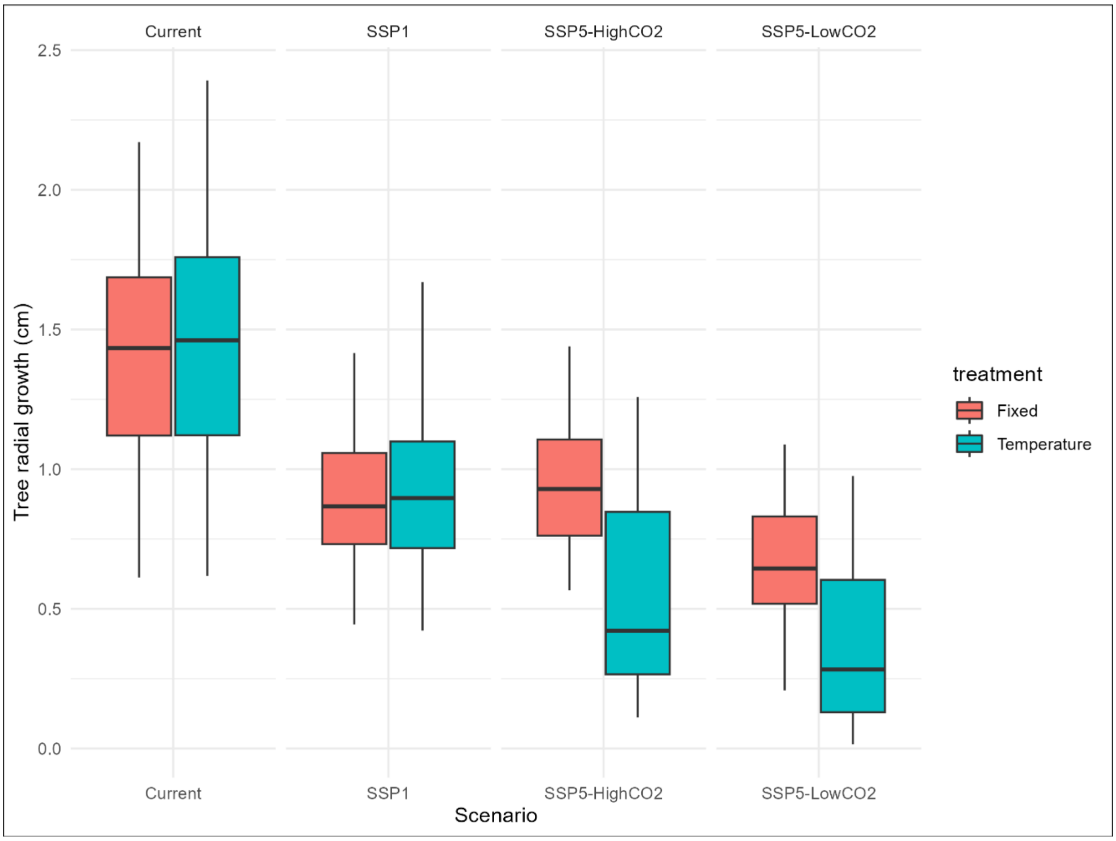

Figure 7 – boxplots of the tree radial growth (cm) per scenario for both a fixed leaf unfolding date (orange) and a temperature-dependent leaf unfolding date (blue).

A possible explanation for the predicted reduction in radial growth due to advanced LU is a shift in allocation patterns. Cambial cell production and reproduction or seed production start right after leaf unfolding, with cambial cell production peaking earlier than reproduction (see the left graph of Figure 8). Advancement of LU could align with earlier cambial activity, causing its peak to occur before the seasonal peak in photosynthetic yield (see the right graph of Figure 8). This shift may result in more assimilates being allocated toward reproduction rather than cambial cell production, leading to a reduction in tree radial growth.

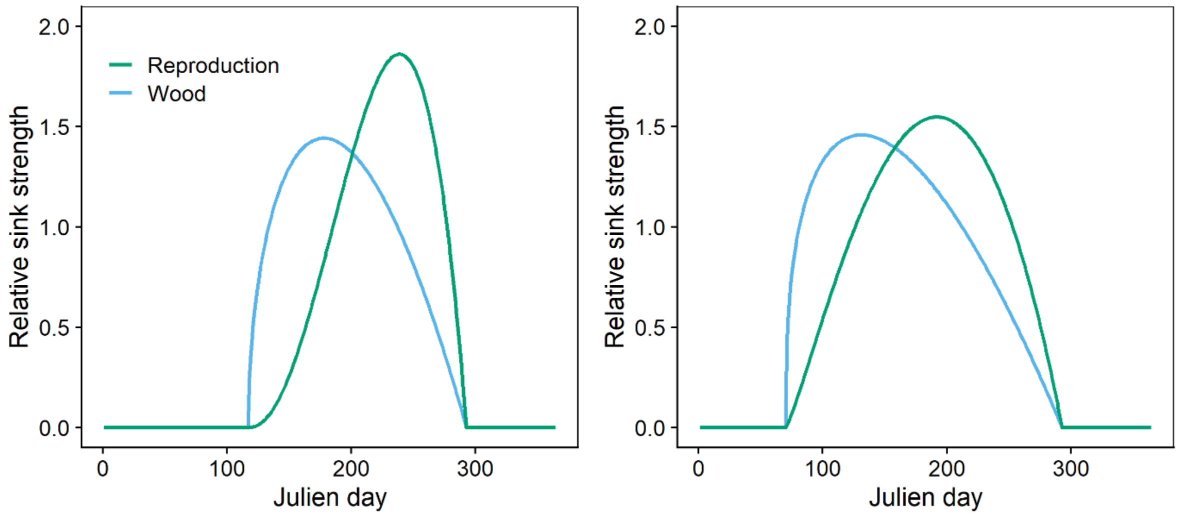

Figure 8 – Relative sink strength of reproduction (green) and wood formation (blue) in a year, with normal allocation patterns in the left graph and the hypothesis of a shift in allocation patterns in the right graph (where LU occurs earlier).

To test this hypothesis, I analysed the ratio between yearly wood and seed production per scenario and per treatment, expecting a lower ratio in the temperature-dependent treatments compared to the fixed treatments. For each scenario and treatment, the average wood-to-seed production ratio is consistent (around 3.5), showing no significant differences between treatments or scenarios and thus there is no shift in allocation (see Figure 9). Instead, there is an overall reduction in biomass production (both wood and seed) with the temperature-dependent LU compared to the fixed LU (Table 19), disproving the hypothesis.

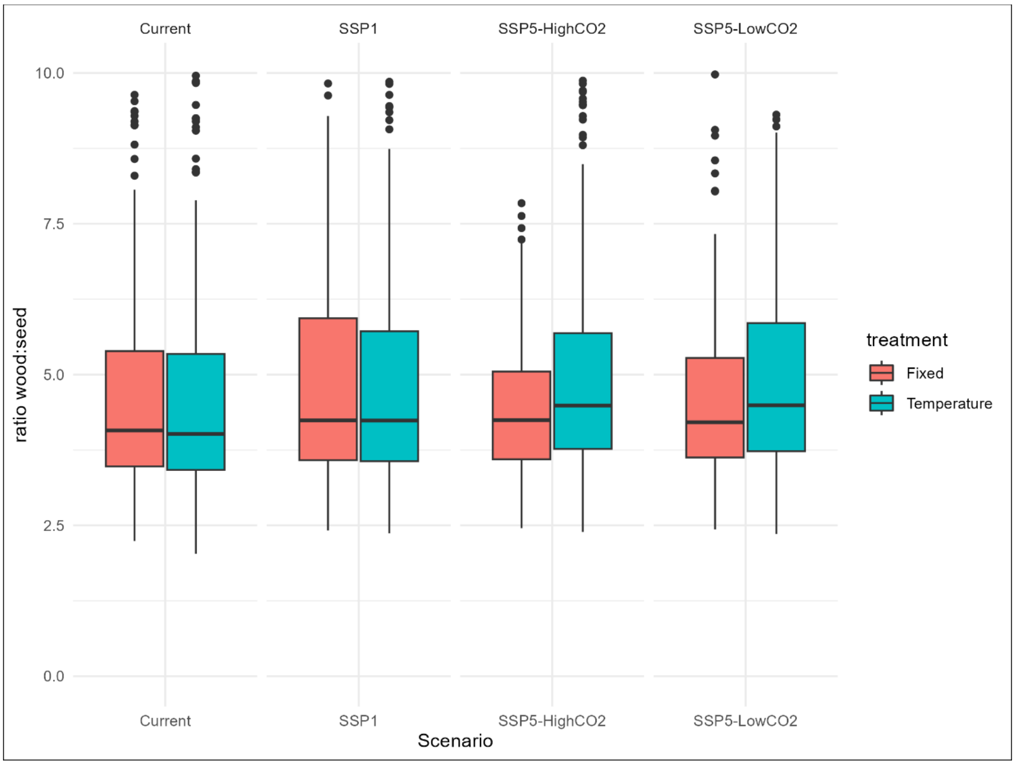

Figure 9 – Boxplots of the ratio between yearly differences in wood biomass and yearly seed production per scenario and for the fixed leaf unfolding date (orange) and temperature-dependent leaf unfolding date (blue).

6. Discussion

Main findings

The results show that a higher temperature in April results in an earlier date of LU for both beech and oak. Additionally, the study demonstrates a positive correlation between the LU date and radial growth of beech, whereas this correlation is negative for oak. The radial growth of beech was positively correlated to and highest for the SPEI in April until June, whereas for oak the SPEI in January until March showed the highest correlation. The combination of SPEI in those months and the LU date explained the tree radial growth the best, indicating that the LU affects the tree radial growth. The results of the FSTree model suggest that the LU date of beech will advance in the future most for the most extreme scenarios (SSP5) and least for the least extreme scenario (SSP1). There was no difference between the SSP5 high and low CO_2 scenario as LU solely depends on temperature in the model. The model also predicted a reduction in radial growth of beech for each scenario, with the biggest reduction for the SSP5 scenarios and least reduction for the SSP1 scenario. There will be slightly less tree radial growth for the SSP5 low CO_2 scenario than for the SSP5 high CO_2 scenario and in both SSP5 scenarios the tree radial growth will decrease more if LU advances.

Relation of leaf unfolding day to temperature

Temperature is the main factor determining LU in temperate climates (Didion-Gency et al., 2023; Vitasse et al., 2011), explaining the high correlations between temperature and LU. In line with my research, Hurbedise et al. (2019) and Didion-Gency et al. (2023) found a negative correlation between spring temperature and the start of the growing season of beech and oak. Similar to my findings, Hurbedise et al. (2019), found that the temperature in April showed the highest correlation with the start of growing season. Although Hurbedise et al. (2019) did not find a trend in increasing temperatures in April, the LU day was clearly advanced in the years with an outstanding warm temperature in April. Under higher temperatures heat accumulates faster, as a consequence the GDD threshold is reached earlier, thus LU occurs earlier (Wenden et al., 2019). Although the research of Wenden et al. (2019) does not mention the influence of the temperature in specific months on tree phenology, similar to my findings, they imply that spring temperature results in an earlier start of the growing season of oak trees.

Future changes in leaf unfolding

Comparable to my findings, Hurbedise et al. (2019) and Wergifosse (2022) expect further advancement of the growing season in the future for oak and beech with increasing spring temperatures. However, these results contradict Wenden et al. (2019) and Fu et al. (2013), who claim that despite warmer temperatures in the future, there will be a limit to the advancement of beech due to the high chilling and photoperiod requirement of beech. This means that beeches require more cold days to exit their dormant state and more days with prolonged daylight hours than oaks before LU can take place (Cole & Sheldon, 2017). With increasing temperatures there will be fewer chilling days, as a consequence the forcing period starts later (Cole & Sheldon, 2017; Wenden et al., 2019), which is the period in which heat accumulates until GDD threshold is reached and LU takes place (Xu et al., 2020). Eventually, photoperiod affects LU to a greater extent than temperature and the warmer spring temperatures cannot make up for the later start of the forcing period, putting a limit to the advancement of LU of beeches (Wenden et al., 2019; Fu, Geng et al., 2019; Cole & Sheldon, 2017; Vitasse & Basler., 2012). Fu, Geng et al. (2019) already observed a notable decrease in the correlation between temperature and LU over recent decades, simultaneously with an increase in the correlation between LU and solar radiation. Although the correlation between LU and temperature was still higher, it implies that indeed photoperiod will become a more important factor with increasing temperatures. Fu, Piao, et al. (2019)

and Cole and Sheldon (2016) suggest that beeches use the photoperiod and chilling days requirement as a way to protect their leaves against potential frost, by not allowing LU to occur earlier.
In this research, only temperature, and not chilling days and photoperiod requirement, was used for the future predictions for the day of LU, which may explain the different outcomes. Nevertheless, the photoperiod and chilling days will likely have more impact on the LU in areas with current warm climates (southern Europe), than in temperate and colder climates (Wenden et al., 2019; Vitasse & Basler, 2012 ; Fu, Geng et al., 2019). It is still unclear to what extent photoperiod and chilling days already affect and will affect LU of beech in the future in the temperate maritime climate of the Netherlands (Vitasse & Basler, 2012; Fu, Geng et al., 2019).

Oaks on the other hand have low chilling and photoperiod requirement compared to beeches, making them more sensitive to spring temperatures and are thus expected to further advance the start of the growing season in the future under global warming (Wenden et al., 2019).

Relation between LU and radial tree growth
In line with my results, Bosela et al. (2018), found a decline in the radial growth of beeches under global warming over the past decades. This decline in radial growth is mainly due to more frequent droughts (Chakraborty et al., 2021; Langer & Busskamp, 2023; Del Castillo et al., 2022).
The small difference between the radial growth with the fixed and temperature-dependent treatment for the current situation and SSP1 scenario could imply that the LU date does not affect the tree radial growth. However, the results of chapter 2 and the SSP5 scenarios suggest the opposite. Likely, the fixed and temperature-dependent LU dates are too similar in both the current situation and the SSP1 scenario to make a significant difference in the radial growth.

A possible explanation for the similar radial growth in the SSP1 scenario and the fixed treatment of the SSP5 high CO_2 scenario is that elevated CO_2 concentrations enhance water use efficiency by limiting transpiration, thereby reducing the adverse impacts of drought on the radial growth of beech. Additionally, beeches may extend their roots during droughts, thereby extracting water from deeper soil layers (Badraghi & Marek, 2020). This reasoning also applies to the slightly lower radial growth in the SSP5 low CO_2 scenario compared to the SSP5 high CO_2 scenario

A hypothesis suggesting a shift in assimilate allocation was proposed and tested to explain why advanced LU might lead to reduced radial growth in beech. The results showed an overall reduction in biomass production instead of a shift, leaving the reason for this overall decrease unclear.

On the contrary to beeches, my findings suggest that an earlier LU for oak results in more radial growth, though the reason for this different effects in oak and beech remains uncertain. Beeches are more susceptible to droughts than oaks (Meyer et al., 2020). These collective findings suggest that oaks are likely to be more resilient to future climate change compared to beeches.

Ecological consequences
Oaks and beeches could suffer from late frost by an advanced LU, causing damage to the leaves, possibly reducing tree growth and endangering pollination in spring (Wergifosse et al., 2022; Vitasse et al., 2009; Nussbaumer et al., 2020). Additionally, inadequate chilling may cause defaults in bud breaks and damage developing acorns and beechnuts, thereby reducing the vitality of oaks and beeches (Wenden et al., 2019; Nussbaumer et al., 2020). Under the impact of climate change, especially beech trees face great threats from more frequent droughts, rising temperatures and high solar radiation. The decline in radial growth of beech due to an advanced LU further decreases the vitality of beeches. Less vital trees are more vulnerable to an increase in attacks by the European beech splendour beetle, sunburns, fungal infections, and complex diseases, resulting in higher tree mortality (Langer &

Busskamp, 2023; Brockerhoff et al., 2017; Brück-Dyckhoff et al., 2019). Nevertheless, oaks are also vulnerable to increased insect outbreaks, such as the gypsy moth, which develops more rapidly under warmer temperatures and already damaged oak forests in Germany (van Vliet et al., 2003).

Tree mortality has tremendous ecological consequences, for example, beech and oak forests provide habitat to a wide range of animal species, so the tree mortality leads to habitat reduction (Schneider et al., 2021). The production of beechnuts and acorns decreases in less vital trees and warmer and drier summers lead to early abortion of beechnuts impacting tree reproduction and food availability for animals (Journé et al., 2021; Nussbaumer et al., 2020). Higher spring temperatures lead to longer canopy duration, which leads to more fruit production for oaks, while beech trees experience peak fruit production when the canopy duration is of moderate length. These distinct relationships in oak and beech trees are likely due to differences in carbohydrate allocation and phenology (Journé et al., 2021). Moreover, high previous summer temperatures boost fruit production, which in turn reduces stem growth as more assimilates are allocated towards reproduction (Hacket-Pain et al., 2018).

Another consequence is that phenological matching, which is the phenomenon where species are dependent on each other's biological recurring events for survival or reproduction, gets disrupted (Cole & Sheldon, 2017). Different species have different phenological responses to climate change, these unequal changes disrupt ecosystem interactions and population dynamics (Cole & Sheldon, 2017; Vitasse et al., 2009; Flynn & Wolkovich, 2018). In temperate deciduous forests, insects depend on the timing of LU for food availability, which subsequently affects insect eating birds. For instance, the abundance of caterpillars relies on the LU of oak trees, therefore great tits have adjusted the timing of their egg laying to the LU of oaks as well. If the abundance of caterpillars advances along with the LU of oaks, but the timing of egg laying of the great tits does not adjust accordingly there is insufficient food available for the great tits, endangering the survival of great tits (Cole & Sheldon, 2017). To conclude, tree mortality and changes in leaf phenology can have great consequences for the survival of various species in different trophic levels.

Limitations

Findings from Vitasse & Basler (2012) found the exact same average LU date (day 117), for long-term data of the European beech in Germany. However, the reliability of the phenology data is impacted by the method of data collection. There is uncertainty about the accuracy of the LU observations as the data was obtained by volunteers. This uncertainty can result in earlier or later average LU dates, especially in years with limited observations. However, to minimize errors, observations after June were excluded, ensuring more accurate results. Although there were no observations between 1969 and 2000, the relatively long periods before 1969 (1900 – 1968) and after 2000 (2001 – 2023) still allow for observing temporal shifts in LU.

Moreover, the LU data and tree radial data are from different trees at different locations, which means that the data is unpaired. The trees might have different ages and environmental circumstances, such as soil type, nutrient and water availability, thus the response (radial growth) of individual trees cannot be confirmed by the data. However, the averages of long-term data of multiple trees, can determine general patterns in the growth dynamics. The outcomes of the FSTree model, where the data was paired, align with the other results, proving the reliability of the unpaired data.

Lastly, the research was restricted by the absence of oak simulations in the FSTree model, so no conclusions could be drawn about the impact of the different climate change scenarios on growth dynamics of oak.

Recommendations

This study contributes to our understanding of how leaf phenology of oak and beech trees might change in the future and how this affects radial growth. To better understand phenological changes and apply forest management effectively, future research should focus on spatial variation and variation in age, considering diverse environmental conditions in the Netherlands.

Moreover, investigating ecological consequences of changes in leaf phenology in more detail is crucial to understand how ecosystems will change in the future. For instance, exploring the link between LU and mast years and how this is expected to change in the future can shed light on reproduction patterns, as well as the availability of food for various animal species. Additionally, understanding how different species will adapt to these phenological changes is essential for predicting shifts in species interactions and conserving beech and oak forests.

Furthermore, it is important to adjust the FSTree model. This includes simulating oak trees to enable predictions for this species as well. Also, further research is needed to establish to what extent photoperiod and chilling days will play a role in the timing of LU of beech trees to improve LU predictions in the model. Adjusting the FSTree model to account for changes in the end of the growing season is also essential for a comprehensive analysis.

Finally, further research is needed to clarify why the radial growth of beech decreases if the LU date advances, while leaf phenology of oak has the opposite effect on radial growth.

7. Conclusion

This research aimed to gain a better understanding of the effects of global warming on the growth dynamics of Pedunculate oak and European beech trees in the Netherlands. The results indicate that the day of leaf unfolding for both oak and beech is primarily influenced by April temperatures, with higher temperatures leading to earlier leaf unfolding, implying further advancement under global warming. This advance of leaf unfolding is also predicted for beech by the FSTree model for all tested climate change scenarios. The least change in leaf unfolding is expected for the low emissions scenario (SSP1) and the strongest change is expected for the most extreme scenarios (SSP5), due to warmer temperatures for the SSP5 scenarios compared to the SSP1 scenario. However, the leaf unfolding of beeches is expected to become increasingly reliant on chilling and photoperiod requirements with further warming, likely putting a limit to the advancement of leaf unfolding. Nevertheless, the extent of the shift of influence of factors on timing of leaf unfolding remains uncertain. Oaks on the other hand are expected to be less dependent on photoperiod and chilling days, indicating that their leaf unfolding will continue to advance in the future. The findings further suggest that an earlier leaf unfolding of oak leads to more radial growth, whereas for beech it has the opposite effect. In line with this result, the FSTree model predicts reduced radial growth in the most extreme scenario (SSP5) when leaf unfolding occurs earlier.

This research suggests that oaks are more resilient to climate change than beeches. These findings enrich our understanding of how forests respond to climate change. Further research is needed to clarify why beech trees experience reduced radial growth with earlier leaf unfolding, while the opposite relationship is found in oak trees.

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9. Appendix methods

Table 1 – Overview of data that was used in this research.

Data	Unit	Years	Extra Info	RQ	Source
Historical **average temperature** data	°C	1901 - 2023	Average per month	1	KNMI - *Maand- En Jaarwaarden,* 2024
Historical **minimum temperature** data	°C	1901 - 2023	Minimum per month	2	KNMI - *Maand- En Jaarwaarden,* 2024
Historical **maximum temperature** data	°C	1901 - 2023	Maximum per month	2	KNMI - *Maand- En Jaarwaarden,* 2024
Historical **precipitation** data	mm	1901 - 2023	Total per month, 1901 – 1905 missing data	2	KNMI - *Maand- En Jaarwaarden,* 2024
Historical **daily temperature** data	°C	01/01/1901 – 22/01/2024	Average per day	3	KNMI – *daggegevens van het weer in Nederland,* 2024
Climate scenarios (KNMI): - **Temperature (minimum, maximum and average)** - **Precipitation** - **Radiation** - **Relative humidity** - **windspeed**	°C mm/day J/m2/day % m/s	Dataset of 1990 - 2020 transformed to 2035 – 2065		3	KNMI - *Klimaatscenario's*, 2024
CO_2 emission scenarios (IPCC)	$GTCO_2$/yr		High and low	3	IPCC, 2023
Leaf Unfolding (oak and beech)	Date (day/month/year)	1900 - 2023	No data between 1969 and 2001.	1, 2, 3.	Nature Today, n.d.
Tree radial growth (oak and beech)	cm	Oak: 1832 – 2020 Beech: 1862 - 2020	Location: Pijbrandje bos reservaat. 15 oak and 15 beech trees, two cores per tree.	2	Dendrochronlogy lab Wageningen University & Research

10. Appendix results

10.1 Appendix RQ1

Table 2 – Correlation coefficients and P-values of correlation tests between Variable 1 (temperature in a certain month) and Variable 2 (the LU date, Julian day) for beech trees.

Variable1 (temperature in month…)	Variable2 (LU day)	Correlation Coefficient	P-value
January	Julian Day	-0.518	2.29E-06
February	Julian Day	-0.561	2.04E-07
March	Julian Day	-0.593	2.65E-08
April	Julian Day	-0.795	2.75E-17
May	Julian Day	-0.308	7.69E-03
June (previous year)	Julian Day	-0.475	2.13E-05
July (previous year)	Julian Day	-0.554	3.73E-07
August (previous year)	Julian Day	-0.435	1.20E-04
September (previous year)	Julian Day	-0.248	3.43E-02
October (previous year)	Julian Day	-0.202	8.61E-02
November (previous year)	Julian Day	-0.291	1.27E-02
December (previous year)	Julian Day	-0.349	2.45E-03

Table 3 - Correlation coefficients and P-values of correlation tests between Variable 1 (temperature in a certain month) and Variable 2 (the LU date, Julian day) for oak trees

Variable1 (temperature in month…)	Variable2 (LU day)	Correlation Coefficient	P-value
January	Julian Day	-0.435	1.06E-04
February	Julian Day	-0.507	3.98E-06
March	Julian Day	-0.651	3.41E-10
April	Julian Day	-0.788	8.66E-17
May	Julian Day	-0.426	1.57E-04
June (previous year)	Julian Day	-0.474	2.29E-05
July (previous year)	Julian Day	-0.546	5.77E-07
August (previous year)	Julian Day	-0.428	1.61E-04
September (previous year)	Julian Day	-0.373	1.15E-03
October (previous year)	Julian Day	-0.29	1.30E-02
November (previous year)	Julian Day	-0.261	2.60E-02
December (previous year)	Julian Day	-0.356	2.01E-03

Table 4 - Correlation coefficients and P-values of correlation tests between Variable 1 (temperature in a certain month) and Variable 2 (the temperature in April) to test autocorrelations.

Variable1	Variable2	Correlation Coefficient	P-value
January	April	0.198	2.91E-02
February	April	0.33	2.18E-04
March	April	0.276	2.22E-03
May	April	0.152	9.67E-02
June (Previous year)	April	0.339	1.50E-04
July (Previous year)	April	0.373	2.66E-05
August (Previous year)	April	0.25	5.98E-03
September (Previous year)	April	0.29	1.31E-03
October (Previous year)	April	0.178	5.19E-02
November (Previous year)	April	0.231	1.12E-02
December (Previous year)	April	0.08	3.84E-01

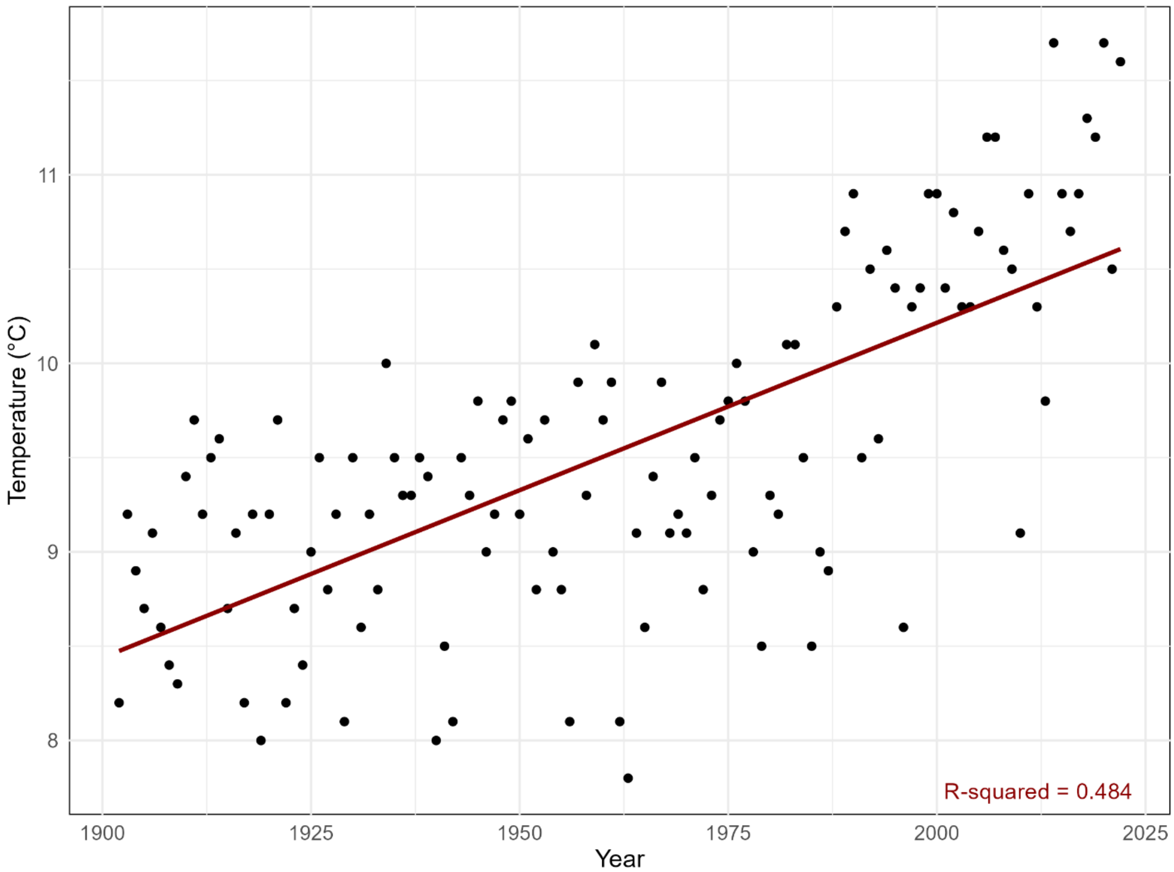

Figure 10 – Average yearly temperature through the years from 1900 until 2023, with the trendline (red line) and R-squared (red number).

10.2 Appendix RQ2

Beech

Table 5 – Correlation coefficients and P-values of correlation tests between Variable 1 (SPEI in a certain month) and Variable 2 (average tree radial growth) for beech trees

Variable1	Variable2	Correlation Coefficient	P-Value
January	Average tree radial growth	-0.019	8.43E-01
February	Average tree radial growth	0.008	9.35E-01
March	Average tree radial growth	0.178	5.65E-02
April	Average tree radial growth	0.328	3.63E-04
May	Average tree radial growth	0.231	1.31E-02
June	Average tree radial growth	0.192	3.94E-02
July	Average tree radial growth	-0.021	8.23E-01
August	Average tree radial growth	-0.054	5.64E-01
September	Average tree radial growth	-0.123	1.92E-01
October	Average tree radial growth	-0.15	1.11E-01
November	Average tree radial growth	-0.082	3.84E-01
December	Average tree radial growth	-0.024	8.03E-01

Table 6 - Correlation coefficients and P-values of correlation tests between Variable 1 (SPEI in three months) and Variable 2 (average tree radial growth) for beech trees

Variable1	Variable2	Correlation Coefficient	P-value
JanMar	TRavg	-0.183	5.06E-02
AprJun	TRavg	0.245	8.43E-03
JulSep	TRavg	-0.003	9.73E-01
OctDec	TRavg	-0.053	5.74E-01

Table 7 - Autocorrelations between SPEI in April-June and SPEI in the other months.

Year	JanMar	OctDec	AprJun	JulSep
-0.004	0.068	-0.022	1	0.008
0.005	0.058	0.188	-0.055	-0.047
-0.009	-0.026	0.1	0.048	-0.053
-0.019	0.081	-0.051	0.071	0.154
0.005	0.11	-0.101	0.205	-0.16
-0.003	-0.051	-0.062	-0.038	-0.056
0.016	-0.087	-0.169	-0.125	-0.185
0.032	0.038	0.114	0.03	0.115
0.008	0.051	-0.109	0.174	-0.072
0.031	0.11	0.047	-0.24	-0.072
0.019	-0.04	-0.173	-0.022	-0.004

Table 8 – ANOVA test results of model 1 until 4 (m1, m2, m3, m4) for beech trees

Model	RSS	Sum of squares	F_Value	P_Value
m1	37.64	NA	NA	NA
m2	37.38	0.26	0.46	4.98E-01
m3	37.38	0.00	0.00	9.47E-01
m4	35.21	2.17	3.89	5.31E-02

Table 9 – ANOVA test result of model 1 and 4 for beech trees

Model	RSS	Sum of squares	F_Value	P_Value
m1	37.64	NA	NA	NA
m4	35.21	2.43	1.45	2.36E-01

Table 10 – ANOVA test result of model 5 and 1 for beech trees

Model	RSS	Sum of squares	F_Value	P_Value
m5	29.30	NA	NA	NA
m1	37.64	-8.34	18.50	5.83E-05

Table 11 – ANOVA test results of model 1 and 6 (m1, m6) for beech trees

Model	RSS	Sum of squares	F_Value	P_Value
m1	37.64	NA	NA	NA
m6	29.30	8.34	18.50	5.83E-05

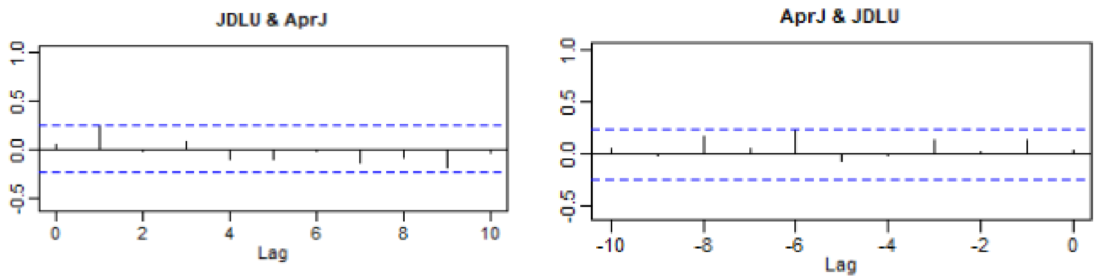

Figure 11 - Autocorrelation test between leaf unfolding day (JDLU) of beech trees and SPEI in April until June with significance level of 0.2 (blue horizontal line).

Oak

Table 12 - Correlation coefficients and P-values of correlation tests between Variable 1 (SPEI in a certain month) and Variable 2 (average tree radial growth) for oak trees.

Variable1	Variable2	Correlation Coefficient	P-value
January	Average tree radial growth	-0.136	1.48E-01
February	Average tree radial growth	-0.039	6.78E-01
March	Average tree radial growth	0.076	4.22E-01
April	Average tree radial growth	-0.225	1.63E-02
May	Average tree radial growth	-0.136	1.50E-01
June	Average tree radial growth	0.131	1.66E-01
July	Average tree radial growth	0.068	4.75E-01
August	Average tree radial growth	-0.002	9.82E-01
September	Average tree radial growth	0.239	1.06E-02
October	Average tree radial growth	0.207	2.71E-02
November	Average tree radial growth	0.171	6.88E-02
December	Average tree radial growth	0.042	6.57E-01

Table 13 - Correlation coefficients and P-values of correlation tests between Variable 1 (SPEI in three months) and Variable 2 (average tree radial growth) for oak trees.

Variable1	Variable2	Correlation coefficient	P-value
JanMar	TRavg	0.309	7.75E-04
AprJun	TRavg	0.115	2.22E-01
JulSep	TRavg	-0.046	6.27E-01
OctDec	TRavg	0.110	2.41E-01

Table 14 - Autocorrelations between SPEI in January-March and SPEI in the other months.

Year	JanMar	OctDec	AprJun	JulSep
0.286	1	-0.03	0.068	0.146
0.264	0.156	0.031	-0.131	-0.292
0.256	-0.004	-0.034	-0.127	-0.124
0.257	0.008	0.15	0.015	0
0.232	0.154	0.259	0.033	0.185
0.213	0.017	0.01	-0.043	-0.05
0.212	0.122	-0.101	-0.044	0.179
0.204	0.033	-0.074	-0.037	-0.028
0.18	-0.099	0.014	-0.019	-0.041
0.161	0.144	-0.026	-0.022	0.032
0.165	0.017	0.083	0.031	0.114

Table 15 - ANOVA test results of model 1 until 4 (m1, m2, m3, m4) for oak trees

Model	RSS	Sum of squares	F_Value	P_Value
m1	9.24	NA	NA	NA
m2	9.16	0.07	0.52	4.73E-01
m3	9.16	0.01	0.04	8.43E-01
m4	8.92	0.24	1.67	2.01E-01

Table 16 - ANOVA test result of model 1 and 4 for oak trees

Model	RSS	Sum_of_sq	F_Value	P_Value
m1	9.24	NA	NA	NA
m4	8.92	0.32	0.74	5.30E-01

Table 17 - ANOVA test result of model 5 and 1 for oak trees

Model	RSS	Sum of squares	F_Value	P_Value
m5	10.43	NA	NA	NA
m1	9.24	1.20	8.55	4.73E-03

Table 18 - ANOVA test results of model 1 and 6 (m1, m6) for oak trees

Model	RSS	Sum of squares	F_Value	P_Value
m1	9.24	NA	NA	NA
m6	8.13	1.11	8.86	4.10E-03

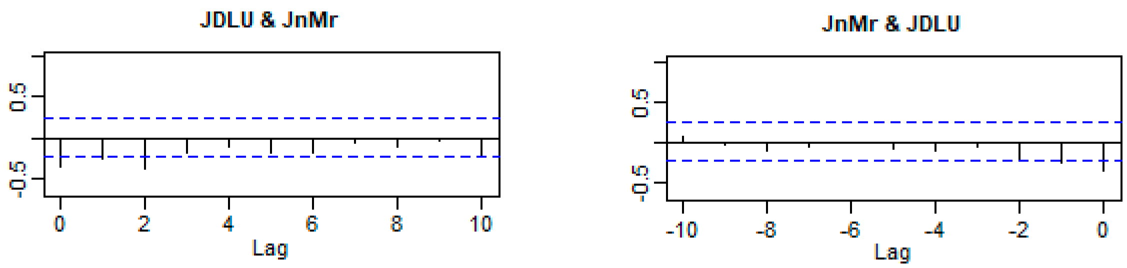

Figure 12 - Autocorrelation test between leaf unfolding day (JDLU) of oak trees and SPEI in January until March, with significance level of 0.2 (see blue horizontal line).

10.3 Appendix RQ3

Table 19 – Average wood biomass, yearly wood production, storage and seed production in grams per scenario and per treatment and the ratio between wood and seed production and between storage and wood

Scenario	Treatment	Wood biomass (g)	Wood production (g)	Storage (g)	Seeds (g)	Wood: Seeds ratio	Storage: Wood ratio
Current	Fixed	3486183.78	79838.12	72708.34	23247.65	3.434	0.0209
Current	Temperature	3480232.19	79061.75	73360.42	23043.97	3.431	0.0211
SSP1	Fixed	3086086.28	48971.33	66071.15	13539.73	3.617	0.0214
SSP1	Temperature	3031275.07	45718.33	65382.32	12762.79	3.582	0.0216
SSP5-HighCO2	Fixed	3317409.87	55778.35	68695.31	15206.36	3.668	0.0207
SSP5-HighCO2	Temperature	2642752.55	25663.64	73176.44	6806.47	3.77	0.0277
SSP5-LowCO2	Fixed	2995882.62	37565.35	64451.69	10244.4	3.667	0.0215
SSP5-LowCO2	Temperature	2756335.06	18748.31	73870.62	5201.88	3.604	0.0268